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The Mammals of the Ardis Local Fauna
(Late Pleistocene), Harleyville, South Carolina

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ABSTRACT—The Ardis local fauna is contained within sediment-filled solution cavities of late Pleistocene age, located in the Giant Cement Quarry near Harleyville, Dorchester County, South Carolina. This paper, the second on the fossil remains collected from the Ardis site, documents 43 taxa of mammals recovered from a group of interconnected solution cavities, including 24 taxa of mammals not previously reported as fossils from the state. Fossil remains from the lowermost layers and the extreme upper layer of the deposit were C^{14} dated at $18,940 \pm 760$ and $18,530 \pm 725$ y.b.p., respectively, and are considered contemporaneous. Fossil remains were deposited near the height of the Wisconsin glaciation and appear to reflect a mosaic edge community, probably a patchwork of mixed hardwood and conifer forest, interspersed with meadows, possibly associated with a marsh or bog, located near a permanent stream or a river. The Ardis local fauna is composed of a mammal community which has no modern analogues ("disharmonious fauna"), and reflects a more equitable climate, cooler summers and warmer winters, than that presently occurring in the region.

INTRODUCTION AND GEOLOGY

As collections of fossils continue to be amassed from various localities in South Carolina, the fossil record of the state likely will be one of the richest in the eastern United States. Long known as a source of marine mammal fossils of Eocene and Oligocene age, the State has a large number of vertebrate faunas from various other time periods. Although the Pleistocene epoch is one of the best represented in South Carolina, only two assemblages (Allen 1926, Roth and Laerm 1980) have been reported in the literature to date.

Our purpose is to present data on a collection of late Rancholabrean mammals, the Ardis local fauna (Appendix 1), found in the Giant

Cement Plant pit near Harleyville, South Carolina. This is the second (Bentley and Knight 1993) in a series of papers that reports the various taxonomic assemblages collected from this site.

The Giant Cement Plant, located about 5 km north-northeast of Harleyville, South Carolina (Fig. 1), is in Dorchester County, about 1 km from Interstate 26 at the Harleyville exit ($33^{\circ}14'N, 80^{\circ}26'W$). It is a large, open-pit mine, in operation for the past 45 years. The stratigraphic assignments for the large exposures of middle Eocene Santee Limestone, which is exploited for cement products, were determined by Sanders (1974), who discussed the marine vertebrate and invertebrate material collected from the pit. Based on reports from Cooke and MacNeil (1952) and Malde (1959), Sanders (1974) refers to the layer which



Fig.1. Location of the Ardis local fauna.

unconformably overlies the Santee Limestone as the "Cooper Marl" of early to late Oligocene age. A more recent survey by Ward et al. (1979) recognizes three members of the "Cooper Marl" (Cooper Formation), the Ashley (Oligocene), the Harleyville (late Eocene), and the Parkers Ferry (late Eocene). The Parkers Ferry and Ashley members were absent at the Ardis fossil locality. Harris and Zullo (1991) refer to the Harleyville member as the Harleyville Formation, and we follow that practice in this paper. Since Sanders' (1974) study, fossil vertebrates of presumed late Pleistocene origin have been collected by workman and hobby collectors from several areas of the quarry, although no stratigraphic assignment could be determined for these fossils. Most were collected from spoil piles of unknown origin.

In April 1991, during a periodic visit to the quarry, the senior author, accompanied by Mr. Vance McCollum, a hobby collector, discovered a newly-mined area in the southeastern wall of the quarry which contained a dense concentration of late Pleistocene terrestrial vertebrate fossils. Giant Cement, in anticipation of further mining operations, had used a dragline to remove overburden from the underlying Santee Limestone. This was done in a single strip which formed a trench at a right angle in the southernmost corner of the pit. This tract of freshly mined earth had a maximum length of about 150 m, a width of 10 m, and a depth of 4 m. Fossils were initially collected from a single row of spoil piles dumped adjacent to the area from which they were mined. We determined that the fossil material came from a series of localized, sediment-filled cavities formed in the underlying Harleyville Formation and Santee Limestone. Groundwater had preferentially dissolved away the upper portions of the Santee Limestone, so that many of the solution cavities contacted the overlying, clay-rich Harleyville Formation. This resulted in the occasional collapse of the Harleyville Formation, opening several of the cavities to the surface.

The diameter of the solution cavities varied from a few centimeters to a maximum diameter of nearly 2.0 m, with many of the cavities interconnected. The solution cavities reached a maximum depth below the Harleyville Formation of about 4 m. The majority of the cavities were infilled with clastic sediment from the surface. The sediment is well stratified and ranges in size from clay to small pebbles. Multiple fining-upward sequences within the cavity-filling deposits indicate episodic sedimentation, perhaps corresponding to flood events within a nearby fluvial system. The undisturbed clay layers within the cavity-filling and the narrow interconnecting nature of the cavities indicate that the entire deposition probably occurred over a relatively short time

span. This tends to be confirmed by the limited range of carbon dates. The Harleyville Formation was capped by a well sorted, cross-stratified quartz sand having a maximum thickness of about 4 m. Fossils collected from this layer were similar to those in the cavities, but fewer in number.

Locally, several cavities which had no connections to the surface were exposed by mining operations in the Santee Limestone. Consequently, these cavities were not infilled from above.

A systematic excavation was not possible because the area at the time of discovery was actively being mined. The operators of the mine graciously relocated their mining operation to another section of the pit, allowing us the maximum possible study time and nearly unlimited access to the fossil deposit. Bert Ardis, an employee of the Giant Cement Plant Company, played a crucial role in the discovery and excavation of fossils from the quarry. In recognition of his efforts the fauna was named in his honor.

DATING OF THE DEPOSIT

Kruger Enterprises, Inc., Cambridge, Massachusetts, used C^{14} dated (C^{13} corrected) mammal and reptile bone apatite to date fossil materials from the lower levels of the solution cavities and from the well-sorted sand layer above the Harleyville Formation. Dating was done on apatite due to the paucity of collagen. The fossil material from the solution cavities (300 g of mixed mammal and reptile bone) were dated at $18,940 \pm 760$ y.b.p. and the fossil material (300 g of mammoth bone), from the overlying unnamed, quartz sand layer (about 1 km from the primary deposit), dated at $18,530 \pm 725$ y.b.p. The overlap of the two dates suggests that the material in the solution tunnels and the homogeneous sand layer above the Harleyville Formation are contemporaneous. These dates place the time of deposition at, or near, the height of the Wisconsin glaciation (Bowen 1988).

Serious questions have recently been raised concerning the reliability of C^{14} dating based on bone apatite and collagen (Stafford et al. 1991). They state that C^{14} dates on noncollagenous bone may yield dates potentially thousands of years too young. Efforts are underway to acquire an amino acid date, even though the apatite sample was apparently very clean (Kruger Enterprises, Inc., personal communication). In light of recent work (Stafford et al. 1991), the C^{14} dates we used will be considered a minimal age for this deposit. The maximum age of the deposit is not expected to exceed 22,000 y.b.p. (Kruger Enterprises, Inc., personal communication). Whatever the date, however, there is little doubt that the fauna represents a late Rancholabrean age, and minor revisions in the absolute dates would have little effect on the ecological or climatic interpretations suggested in our paper.

METHODS

All fossil material reported here was collected during periodic trips into the quarry by the authors and a group of volunteers. We collected fossil material from the surface of associated spoil piles as well as by screen sifting the fossiliferous sand. Screens used were 20 gauge (1.0 mm) to quarter-inch (6.35 mm) mesh. Materials in situ were collected by a combination of screen-washing and by applying a gentle, controlled stream of water to the exposed sands. Fossils were exposed as the sand was gently washed away.

Most specimens from the Ardis local fauna were deposited in the South Carolina State Museum collections and are registered under the accession base number of S.C. 93.105. We cite such specimens in this paper only by the numbers following that base number. Fossils that were accessioned separately in the South Carolina State Museum's collections will be designated by S.C. followed by five to six digits. Fossil specimens deposited in the National Museum of Natural History have been accessioned under the number of 407498 and are indicated by an institutional prefix of USNM in the text. Fossil material deposited at the Florida Museum of Natural History will be referred to by an institutional prefix of UF.

Taxonomy for extant and extinct taxa follows Wilson and Reeder (1993) and Kurten and Anderson (1980), respectively. Common names were taken from Webster et al. (1985), and Kurten and Anderson (1980). Under Materials, capital "M" denotes upper dentition, lower case "m" denotes lower dentition.

SYSTEMATICS

Class Mammalia

Order Didelphimorphia

Family Didelphidae

Didelphis virginiana - Virginia Opossum

Material: 1 left dentary with m1 and m2 and an unerupted p3 (.1); 1 left dentary with m2 and m3 (.2); 1 left maxilla fragment with P3 and M1 (.3); 1 right M3 (.8); 1 right M1 (.9); 6 right partial dentaries (3 USNM & 3 UF); 1 left dentary, proximal one third (USNM); 1 right proximal dentary fragment (USNM); 4 left humeri, distal ends (.4-.7).

Remarks: The opossum is found throughout most of the United States and northward into Canada. Late Pleistocene fossils are restricted to the southern parts of the United States, and the species is believed to have radiated into the northern part of the continent during historical times (Kurten and Anderson 1980). The species is common today in the vicinity of the Ardis locality.

This is the first published report of fossil *D. virginiana* from South Carolina.

Order Xenarthra
Family Megalonychidae
Megalonyx jeffersoni - Jefferson's Ground Sloth

Material: 1 upper right 3rd molariform (.194).

Remarks: This sloth has been found as far north as Canada and the western coast of Alaska, and formerly ranged throughout the United States except for the Rocky Mountains, Great Basin, and the arid or desert areas of the Southwest. It is thought that the diet of this sloth consisted of twigs and leaves and that it inhabited forested or wooded areas (Kurten and Anderson 1980).

Previous reports of this species from South Carolina include Hay (1923) and material from Edisto Island (Roth and Laerm 1980).

Family Dasypodidae
Dasypus bellus - Beautiful Armadillo

Material: 25 buckler osteoderms (.200- .210), (5 USNM), (9 UF); 11 movable osteoderms (.195- .199), (3 USNM), (3 UF); 1 cephalic osteoderm (.211); 1 caudal vertebra (.212).

Remarks: This armadillo probably fed primarily on insects and that diet might have restricted its range to moderate climes (Kurten and Anderson 1980). However, Voorhies (1987) questioned its reliability as a warm weather indicator. Its occurrence with mostly boreal forms in the Craigmile local fauna, Nebraska (Rhodes 1984), suggests that it may have been able to withstand weather conditions considerably cooler than *D. novemcinctus*. *D. bellus* fossil records are well established in South America and the southern portions of the United States (Kurten and Anderson 1980). This suggests that *D. bellus* is a fairly reliable indicator of warm climates, and the material from Nebraska may represent a fringe population. Although a common Pleistocene fossil, this is only the second report of this species from South Carolina. It was first reported by Roth and Laerm (1980) from Edisto Island.

Family Pampatheriidae
Holmesina septentrionalis - Northern Pampathere

Material: 1 partial buckler osteoderm (.227); 1 cephalic osteoderm (.228).

Remarks: Differentiation of the cephalic and buckler osteoderm was based on the descriptions of Edmund (1985).

Little is known about its diet, which probably consisted of coarse vegetation (based on large, flat, high-crowned teeth of indeterminate growth). Regarding its habitat, *Holmesina* is suspected to be intolerant of cold climates (Kurten and Anderson 1980).

Holmesina was first reported from South Carolina by Roth and Laerm (1980) at Edisto Island.

Order Insectivora

Family Soricidae

Blarina brevicauda - Northern Short-tailed Shrew

Material: 2 right maxillae with the M1 and M2 (.11, .12); 4 right dentaries with m2 and m3 (USNM); c1, p1, p2, m1, m2 (.13); c1, m1 (.14); c1, p1, p2, m1 (.15), respectively; 2 left maxillae with M1, M2, M3 (.16) and M1 (.17) respectively; 1 left dentary with m1-m3 (.18); 1 isolated c1 (.19).

Remarks: Identification was made on the basis of characters listed by Guilday (1962) and by direct comparisons to fossil and recent specimens. Ardis specimens are indistinguishable from modern comparative materials of *B. brevicauda* and are generally larger in size than samples of *B. carolinensis* (Graham and Semken 1976). Apparently *B. brevicauda* size reflects a positive Bergmann's response, suggesting that the fossils from the Ardis site are a more northerly stock and not the smaller southern species *B. carolinensis* (McNab 1971, Guilday et al. 1977, Klippel and Parmalee 1982, Jones et al. 1984).

The northern short-tailed shrew occurs in a variety of terrestrial habitats from forests, fields and meadows, to salt marshes. Today this species occurs, in South Carolina, only in the extreme northwestern portion of the State, nearly 300 km from the fossil locality. An isolated population on the coast of North Carolina is about the same distance from the site (Webster et al. 1985). *B. carolinensis* does occur in the area of the Ardis site today.

This is the first fossil record of *B. brevicauda* reported from South Carolina.

Sorex sp. cf. *S. longirostris* - Southeastern Shrew

Material: 1 left dentary with complete dentition (.10).

Remarks: Guilday (1962) and Guilday et al. (1969, 1977) separated *Sorex cinereus* from *S. longirostris* based on a slightly larger mean size of *S. cinereus*, because tooth morphology is nearly identical. The

P4-M3 measurement of our specimen (3.64 mm) fell at the bottom of the range for *S. cinereus* and below the mean given for that species at both New Paris Cave No.4, Pennsylvania, and Clark's Cave, Virginia (Guilday 1964, Guilday et al. 1977). Because the Ardis local fauna contains many extralimital species, both northern and southern, and because of the morphological ambiguity between *S. longirostris* and *S. cinereus* (Jones et al. 1991), the fossil specimen from the Ardis site is tentatively assigned to *S. longirostris* and not *S. cinereus*, as only the former occurs in the area of the Ardis site today. The *Sorex longirostris* P4-M3 measurement is considerably larger than that of *S. hoyi* (Guilday et al. 1977).

At present the southeastern shrew ranges from southeastern Arkansas, east to central Florida, and north along the Atlantic coast into Maryland. It is associated with moist, open fields and lowland forests but can also be found in dry upland fields (Webster et al. 1985). In the late Pleistocene this shrew has been reported only from the late Rancholabrean Haile 11B and Arredondo sites in northern Florida (Kurten and Anderson 1980, Webb and Wilkins 1984). The Ardis site is the first identification of this shrew from the Wisconsin time period and from South Carolina.

Family Talpidae

Condylura cristata - Star-nosed Mole

Material: 3 humeri (.20-.22).

Remarks: Identification was made by comparisons to recent specimens. Humeri of this species differ from those of *S. aquaticus* in having a less robust humeral shaft and a smaller width at both proximal and distal ends.

At present *C. cristata* occurs in the upland and the Coastal Plain of South Carolina but is absent from the midland area. The star-nosed mole is an excellent swimmer and inhabits areas that have moist soils or are located near water (Webster et al. 1985). It may be found in wooded areas, meadows or fields, swamps, and bogs. Today, it is found in the area of the Ardis site.

This is the first fossil report of this mole from South Carolina.

Scalopus aquaticus - Eastern Mole

Material: 16 humeri (.23-.26), (6 USNM), (6 UF).

Remarks: These humeri are separated from other South Carolina mole species on the basis of their greater robustness, which may reflect a more fossorial life style.

The eastern mole ranges from the eastern to midwestern United States, commonly inhabiting well-drained sand or loam soil types, and less common in clay or gravel soils (Webster et al. 1985). Eastern moles are found today in the vicinity of the fossil site.

This is the first fossil record of this species for South Carolina.

Order Carnivora

Family Canidae

Urocyon sp. cf. *U. cinereoargenteus* - Gray Fox

Material: 1 metapodial (.254).

Remarks: Felid metapodial elements are generally more robust and have a more acute curvature to the shaft in comparison to modern canid specimens in the Florida Museum of Natural History collections (Gary Morgan, Florida Museum of Natural History, personal communication). The proximal articulation varies significantly from all felids examined and most closely parallels those of canids. The curvature of the elongated shaft, overall size, and simple articulations of the proximal end suggest a close affinity to *U. cinereoargenteus*. A small convexity dorsal and anterior to the proximal articulation was the most significant variation between the fossil element and recent specimens of the gray fox.

Roth and Laerm (1980) refer an Edisto Beach ulnar fragment to this species but state that it may be recent.

Canis dirus - Dire Wolf

Material: 1 brain case (SC 91.171.1); 1 left c1 (.251); 1 metapodial shaft (.252); 1 left jugal (.253).

Remarks: The dire wolf is one of the more common late Pleistocene canids recovered from North American fossil sites (Kurten and Anderson 1980). The material recovered from the Ardis site is believed to represent "wash-ins," as many of the elements, particularly the brain case, show signs of weathering and abrasions prior to fossilization. This represents the second reported occurrence of the dire wolf from this State, as *C. dirus* was reported from Edisto Island (Roth and Laerm 1980).

Family Felidae

Subfamily Machairodontinae

cf. *Smilodon fatalis*. - Sabertooth

Material: 1 left occipital condyle (.266).

Remarks: The shape and size of the condyle has its closest affinities with *Smilodon* and differs significantly from any other large mammal. The identification is extremely tenuous, however, and after an exhaustive search, represents the best possible solution to the identification of this specimen.

Subfamily Felinae

Lynx rufus - Bobcat

Material: 1 right dentary lacking teeth, proximal end missing behind m3 alveoli (.267).

Remarks: This specimen is extremely similar to mandibles of *Lynx rufus* especially in general ramus shape, and alveolar count and placement. The bobcat inhabits a range of habitats including deserts, swamps, and upland forests (Kurten and Anderson 1980), and it occurs in the Ardis local fauna area today (Webster et al. 1985).

This is the first fossil record of *Lynx rufus* from South Carolina.

Family Mustelidae

Subfamily Lutrinae

Lontra canadensis - River Otter

Material: 1 cranium missing the right zygomatic arch and retaining only the left P1-M1 (SC 91.116.1); 1 atlas vertebra (.242); 1 caudal vertebra (.243).

Remarks: The river otter once occurred throughout the United States, including Alaska, but has been extirpated from many areas of the Midwest and Appalachian Highlands. The otter occurs sparsely throughout South Carolina, inhabiting a wide range of aquatic habitats. It appears to be most abundant in coastal estuaries and the lower reaches of rivers in the State (Webster et al. 1985).

This is the first fossil record of this taxon from South Carolina.

Subfamily Mephitinae

Spilogale putorius - Eastern Spotted Skunk

Material: 1 proximal end of the right dentary with the alveoli for a partial m2 and for the m3 (.244).

Remarks: The partial dentary was differentiated from *Mustela vison* because the condyle tapers to a point lingually, whereas it is blunt in *Mustela vison*. The ramus of *Spilogale* is generally smaller and less robust, is laterally compressed, and lacks the distinct curvature found in mink. It also lacks the flattened ventral proximal edge found in the dentary of mink. It differed from other mustelids in the shape and size of the M2 alveoli and overall jaw size and shape. It is significantly smaller than skunks of the genera *Conepatus* and *Mephitis* and is most similar to *Spilogale* in size and general jaw morphology.

The eastern spotted skunk is found typically in prairies, brushy open forests, and mountain habitats. They no longer occur in the immediate area of the fossil site and are found sparsely in the Piedmont of South Carolina today (Webster et al. 1985).

This represents the first fossil record of this species from the State.

Mephitis mephitis - Striped Skunk

Material: 1 partial right dentary containing the alveoli of the m3 (.245); 1 left M1 (.256).

Remarks: The partial dentary was assigned to this species based on the length of the third molar and the presence of auxiliary roots. The overall size of the dentary was intermediate between *Spilogale* and *Conepatus*.

The striped skunk is found in the area of the site today and throughout much of North America and well into Central America (Hall 1981). It can be found in habitats varying from high mountain forests to brushy, semi-open areas, but appears to be much less common in wetlands (Webster et al. 1985).

This is the first report of the striped skunk in the fossil record from South Carolina.

Conepatus sp. cf. *C. robustus* - Extinct Hog-nosed Skunk

Material: 1 humerus (.247); 1 femur (.248); 1 partial dentary with p3 and alveoli of m1 (.249); 1 astragalus (.250).

Remarks: The fossil remains have been referred to this species based on their extremely large size in comparison with the living hog-nosed skunk *Conepatus leuconotus* (Martin 1978). The Ardis fossils exhibit a 30% size increase over *C. leuconotus*. No definable differences were observed between the Ardis material and the type of *C. robustus* from

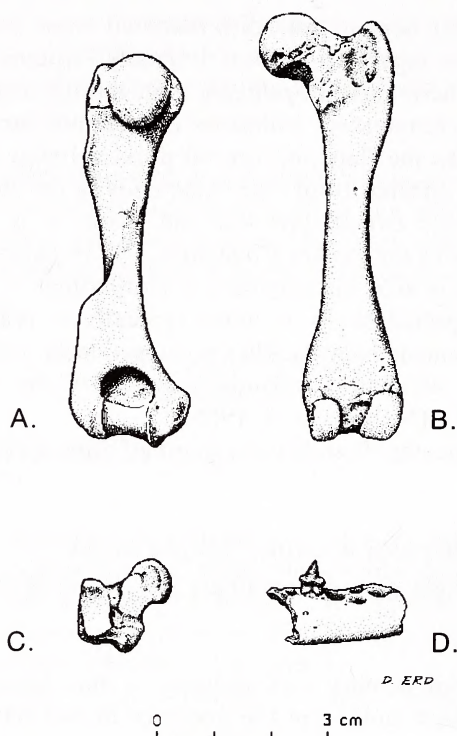


Fig. 2. *Conepatus* sp. cf. *C. robustus* material recovered from the Ardis local fauna. A) Humerus B) Femur C) Astragalus D) Dentary with p3.

the late Rancholabrean Haile 14 in Florida (Martin 1978). The femur and astragalus are the first of these elements to be reported for this species and were assigned based on morphology and their large size (Fig. 2). The extant species inhabit the southwestern United States, southward into Central America, and as far east as eastern Texas (Hall 1981).

This is the first report of this species from South Carolina and the first fossil record of this extinct hog-nosed skunk from outside of Florida.

Subfamily Mustelinae

Mustela vison - Mink

Material: 1 left dentary, complete dentition except for incisors (1 USNM); 1 left dentary, complete dentition except for incisors and

canine (.229); 1 partial maxilla with P3 and M1 and partial zygomatic arch (.231); 2 canines (.232, .233); 1 left dentary with p3 and m1 (.230); 1 left dentary with alveoli p2-m2 (.234); 1 left dentary (in the private collection of Lee Hudson, Florence, S.C.); 2 right ulnae (.235, .236); 1 thoracic vertebra (.237); 1 lumbar vertebra (.238); 1 right 3rd metatarsal (.239); 1 left 2nd metatarsal (.240); 1 rib (.241).

Remarks: Mink remains are generally uncommon in Pleistocene deposits (Kurten and Anderson 1980), but it was the most common carnivore at the Ardis site. This abundance might be explained by its relatively small size and ability to enter cavities that may have excluded larger carnivores. Mink may have also been attracted to favored prey items, in particular a large muskrat population which was using the cavities for various reasons. Muskrats are commonly fed upon by mink, and during certain times of the year, depending on availability, make up the bulk of their diet (Proulx et al. 1987). Mink are good indicators of nearby bodies of water and are found in a variety of habitats bordering water including rivers and streams, swamps, drainage ditches, marshes, and lakes (Webster et al. 1985). Mink are not abundant in South Carolina today, although they probably occur in the area of the Ardis site.

This is the first reported fossil record of this species from South Carolina.

Family Procyonidae
Subfamily Procyoninae
Procyon lotor - Raccoon

Material: 1 left dentary with m3 present and m1 alveoli (.255); 1 left dentary with p4-m2 alveoli (.256); 1 left m1 (.257); 1 right proximal end of dentary with m2 alveoli (.258); 1 left humerus shaft with partial distal end (.259); 1 left humerus distal end (.260); 1 right ulna proximal end (.261); 1 right humerus partial distal end (.263); 1 radius distal half (.262).

Remarks: The distribution of the raccoon is from Panama north through Mexico and the United States into the central portions of Canada (Hall 1981). Its habitat is ubiquitous, but is generally in or near forested wetlands such as stream and river bottoms, marshes, swamps, ponds, and lakes as well as upland and agricultural areas (Webster et al. 1985). Fossil remains of *P. lotor* are generally common in the United States during the late Pleistocene, especially in sinkhole and cave deposits (Kurten and Anderson 1980). The first South Carolina fossil of the raccoon was reported from Edisto Island (Roth and Laerm

1980), based on mandibular fragments and postcranial remains. The material from the Ardis local fauna represents the second report of fossil *P. lotor* from South Carolina.

Family Ursidae

Tremarctos floridanus - Florida Cave Bear

Material: 1 right m3 (.264); 1 first right metatarsal (.265)

Remarks: The m3 of *Tremarctos floridanus* differs from *Ursus americanus* in that it lacks the double root, and is substantially smaller than any other ursid in the eastern United States. The Florida cave bear has been recovered from Rancholabrean sites in Florida, Georgia, Tennessee, Kentucky, New Mexico, Texas, and northern Mexico (Kurten and Anderson 1980). Based on the fossil record it would appear that the Florida cave bear had a more southeastern distribution during the late Pleistocene. The material from the Ardis local fauna represents the second report of this species (Roth and Laerm 1980), from South Carolina. Both reports are from deposits along the Coastal Plain of the State.

Order Proboscidea

Family Mammutidae

Mammut americanum - American Mastodon

Material: 1 partial milk tooth (.332); 2 partial molars (.333, .334).

Remarks: The American mastodon was first reported in the fossil record for South Carolina from Edisto Island by Roth and Laerm (1980).

Family Elephantidae

Mammuthus columbi - Columbian Mammoth

Material: 1 complete molar (.335); partial molar (.336); partial scapula (in the collections of Lander University).

Remarks: All identifiable *Mammuthus* remains from the area of the Ardis local fauna have been recovered from the quartz sand layer above the Harleyville clay, and not in direct association with the Ardis fauna proper. Identification is based on the lamellar frequency (7) of the occlusal surface coupled with the late Pleistocene date of the site (Kurten and Anderson 1980). Carbon dating of the bone from a scapula associated with a complete and a partial molar of *M. columbi* gave a date of $18,530 \pm 725$ y.p.b., within the range of the Ardis local fauna and here considered contemporaneous with it.

All other *Mammuthus* material reported previously from South Carolina has been assigned to *M. columbi* as well (Hay 1923, Allen 1926, Roth and Laerm 1980).

Order Proboscidea
gen. et spec. indet.

Material: 1 distal fragment of tibia (.337); 1 vertebra (.340); 1 proximal rib end (.338); 6 fragments of ivory (.339a-c), (3 USNM).

Remarks: Identification to a particular family is not possible because of the fragmentary nature of these remains. Because the openings of the solution cavities to the surface were small, and large mammals are only represented by isolated fragments, these animals probably died on the surface nearby and were washed in by periodic flooding.

Order Perissodactyla
Family Equidae

Equus cf *E. complicatus* - Complex-toothed Horse

Material: 2 partial incisors (2 USNM); 1 left M1 or M2 (1 USNM); 1 left DP3 or DP4 (.320); 1 right P3 or P4 (.319); 2 right M3s (1 USNM), (1 UF); 1 left m3 (1 USNM); 1 canine (.322); associated-1 axis, 3 caudal vertebrae, 1 incisor, and 3 rib fragments (.321a-h); 1 left distal radial end (.323); 1 right fourth metatarsal (.324); 1 left second metacarpal (.331); 2 left cuneiforms (.325, .326); 1 right magnum (.327); 1 right lunar (.328); 2 medial phalanx (.329, .330).

Remarks: The *Equus* cheek teeth from the Ardis local fauna have been tentatively assigned to the species *E. complicatus* based on the extremely complex nature of the occlusal surface. All other remains, because of the ambiguity in postcranial elements between *E. complicatus*, *E. fraternus*, and *E. occidentalis*, are referred to only as *Equus* sp.

Fossil remains assigned to the genus *Equus* were reported from South Carolina by Hay (1923), Allen (1926), and Roth and Laerm (1980).

Family Tapiridae
Tapirus veroensis - Vero Tapir

Material: 1 partial right m3 (1 USNM); 1 partial m2 (UF); 2 partial left m3 (.316, .317); 1 partial right molar (.318).

Remarks: Tapir remains are among the more commonly collected Pleistocene fossils in South Carolina. Several tooth fragments referred to *T. haysii* were reported by Allen (1926) and represent the first record of tapir from South Carolina. Roth and Laerm (1980) reported numerous tooth fragments and some postcranial material from Edisto Island, but because of the fragmentary nature of the fossils, were unable to assign them to species. A virtually complete skull of *T. veroensis*, reported on by Ray and Sanders (1984), was collected by a diver in the Cooper River near Charleston, South Carolina. The material from the Ardis site is referred to *T. veroensis*, based on the generally smaller size of the molars in comparison to *T. haysii*. Extant species are semiaquatic browsers having a Neotropical distribution, with North American fossil localities suggesting a distribution south of glaciated areas during the Pleistocene (Kurten and Anderson 1980).

Order Artiodactyla

Family Tayassuidae

Mylohyus nasutus - Long-nosed Peccary

Material: 1 right dp2 (.306); 1 m1 or m2 (.307).

Remarks: This species, referred to as *M. pennsylvanicus*, was first reported from South Carolina by Allen (1926). Fossils from Edisto Island were referred to as *M. cf. M. fossilise* by Roth and Laerm (1980). Both names are synonyms of *Mylohyus nasutus*, following Kurten and Anderson (1980).

Family Camelidae

Palaeolama mirifica - Stout-legged Llama

Material: 1 partial lower molar (.268); 1 partial upper molar (.269); 1 left ectocuneiform (.270); 1 phalanx distal end (.271); 1 phalanx proximal two-thirds (.272); 1 hoof core (.273); 1 partial calcaneum (.274); 1 thoracic vertebra (.275); 1 metatarsal 3&4 proximal end (.276); 1 astragalus (.277).

Remarks: Identification was based on the presence of a weak "llama buttress" on the lower molar, and a weakly developed styloid (Webb 1974b), and a low crowned cheek tooth. Distinctive postcranial remains were compared directly to other camelid material.

It appears that the northern limits of this stout-legged llama were generally restricted to low temperate latitudes, e.g., southern California, the Gulf Coast of Texas, and Edisto Island, South Carolina (Roth and Laerm 1980), although it has been recorded in Missouri as

well. It is thought that the diet of this llama consisted of grasses as well as the shoots and leaves from bushes and trees (Kurten and Anderson 1980). The Ardis local fauna is the second report of this species from South Carolina.

Family Cervidae
Subfamily Odocoileinae

Odocoileus virginianus - White-tailed Deer

Material: 1 left M1 (.278); 1 left m1 (1 USNM); 1 right M1 (.282); 1 right M1 (1 USNM); 1 left P3 (.279); 1 right p3 (1 UF); 1 right P1 (.283); 1 right m3 (.284); 1 left m2 (1 UF); 2 dm's (.280, .281); 1 left P2 (1 USNM); 1 right scapula proximal end (.285); 1 humerus distal end (.305); 1 distal end of calcaneum (.286); 1 astragalus (.287); 3 cubonavicular (.288, .289), (1 USNM); 1 right scaphoid (.290); 1 trapezoidomagnum (.304); 1 ectocuneiform (.315); 2 right proximal ulnas (.291, .292); 1 sacral vertebra (.293); 2 distal right radii (.294, .295) and 1 right radius of sub-adult (.296); 1 left proximal tibio-fibula (.297); 1 ulna partial proximal end (.298); right articulated (2) metatarsus and hoof core (.299a-c); 1 right metacarpal (.300); 1 right rib proximal end (.301) and 1 unspecified rib proximal end (.302); 1 right partial antler including the burr and past first two tines both of which are missing (1 USNM); 1 right antler (.303).

Remarks: The first fossil record of *O. virginianus* reported from South Carolina was based on two basal antler fragments (Allen 1926). A second record exists from Edisto Island (Roth and Laerm 1980), based on antler fragments and other postcranial remains, but these may be of recent origin. The white-tailed deer ranges from Canada into northern South America, but is absent from hot arid areas of North America. It occupies a wide variety of habitats today, including coniferous and deciduous forests, high mountain areas, coastal marshlands, grasslands, and suburban fringes. It is most commonly found in broken habitats typical of agricultural areas (Webster et al. 1985).

This deer is very common around the Ardis site today. The Ardis local fauna appears to have individuals from several different age cohorts, based on tooth wear patterns.

Family Bovidae
Subfamily Bovinae
Bison antiquus

Material: 1 right m2 (UF); 1 left P4 (.308); 1 left M2 (.309); 1 left p3 (.310); 1 left p2 (.311); 1 right M3 (USNM); 1 left m3 (.312); 2

lumbar vertebrae (.313), (USNM); 1 metacarpus (.401); 1 lunar scaphoid pisiform (.314); 1 neural process (USNM), 1 right hoof core (S.C. 92.22.1).

Remarks: Leidy (1860) reported the first bison material from South Carolina, as *B. latifrons*. Hay (1923) mentions a fossil which he refers to as *Bison* sp., and Allen (1926) identified a single molar as *Bison* sp. cf. *B. bison*. Allen also mentions a horn core and suggests that it belongs to a bovid. The Edisto Island fossil assemblage (Roth and Laerm 1980) contains bison material and is identified only as *Bison* sp. The molars and postcranial material from the Ardis site are assigned to *B. antiquus* based on size. These specimens are larger than modern *B. bison* and comparable in size to *B. antiquus*.

This is the first report of *Bison antiquus* from South Carolina.

Order Rodentia
Family Sciuridae

Glaucomys volans - Southern Flying Squirrel

Material: 1 left femur (.171).

Remarks: The specimen, a femur broken just below the distal end, is assigned to *G. volans* based on the length of the shaft compared to the width of the proximal end, and overall smaller size compared to *G. sabrinus*.

This species is found commonly today in the eastern United States. It ranges as far north as Canada and southwest into Mexico and Guatemala (Kurten and Anderson 1980).

Typical habitats are deciduous and mixed hardwood forests. *Glaucomys* fossils found in the southeastern United States are commonly collected from cave deposits frequented by birds of prey during the time of deposition (Guilday 1962; Guilday et al. 1969, 1977, 1978; Grady and Garton 1982). The femur is believed either to have been "washed in" or carried by a non-avian predator. There is no evidence of regurgitated pellets from roosting raptors, and the entrances and the chambers of the solution tunnels throughout the site were too small to facilitate large roosting birds.

This represents the first fossil evidence of a southern flying squirrel in South Carolina.

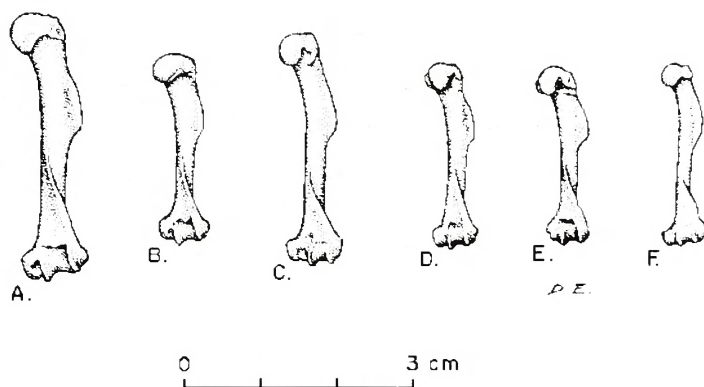


Fig. 3. Comparisons of recent squirrel humeri to the Ardis fossil specimen. A) *Spermophilus franklini* (USNM-54153) B) *Spermophilus lateralis* (USNM-250744) C) *Tamiasciurus hudsonicus* (USNM-505592) D) *Spermophilus tridecemlineatus* (USNM-255383) E) *Spermophilus tridecemlineatus* Ardis local fauna (.175) F) *Tamias striatus* (USNM-347965).

Sciurus carolinensis - Gray Squirrel

Material: 1 right humerus proximal half (.172); 1 right tibia proximal half (.173); 1 left tibia distal one third (.174).

Remarks: The material is distinguished from *Sciurus niger* by its smaller size and is indistinguishable from recent material of the gray squirrel. This species ranges throughout the eastern half of the United States north into Canada, where it inhabits deciduous and coniferous forests, timbered streams, and bottomlands (Webster et al. 1985).

This is the first fossil record of the gray squirrel from South Carolina.

Spermophilus tridecemlineatus - Thirteen-lined Ground Squirrel

Material: 1 left humerus (.175).

Remarks: In comparisons with recent humeri of mustelids, microtines, cricetids, and a variety of ground squirrels, all others were eliminated because of various morphological inconsistencies. *Tamias striatus* humeri vary significantly from *S. tridecemlineatus* with differently shaped proximal condyles and distal articulations. The humeral shaft is noticeably more slender with respect to the total length in *Tamias striatus* than in *S. tridecemlineatus*. *Tamiasciurus hudsonicus* humeri have a

broader distal end and are considerably larger than *S. tridecemlineatus*. The humerus of *S. franklinii* is significantly larger (2x) and varies morphologically from *S. tridecemlineatus*. The fossil humerus is indistinguishable from that of *Spermophilus tridecemlineatus* and given geographical and temporal considerations is assigned to this species (Fig. 3).

The thirteen-lined ground squirrel has a modern range reaching into central Canada, south into eastern Utah and central Texas, and eastward through the Midwest into Ohio (Hall 1981). The fossil specimen from the Ardis site is about 1,000 km southeast of its present day distribution. *S. tridecemlineatus* inhabits shortgrass prairies and does not occur in forested areas (Kurten and Anderson 1980). Clark's Cave and Natural Chimneys, Virginia, and Baker Bluff Cave, eastern Tennessee, are the closest fossil localities containing remains of *S. tridecemlineatus*. Martin and Webb (1974) reported *Spermophilus* sp. from Haile 14A in Florida, which is the most southeastern report of this genus. This ground squirrel's presence in the East has been interpreted as indicating parkland or semi-prairie conditions (Guilday et al. 1977, Kurten and Anderson 1980).

This is the first fossil record of *Spermophilus tridecemlineatus* from South Carolina.

Family Castoridae

Castor canadensis - Beaver

Material: 1 left M3 (.176); 1 partial incisor (.177); 1 left M2 (.178); 1 radius (.180); 1 tibio-fibula distal end (.179); 1 metatarsal (.193); 1 phalanx (.181); 1 thoracic vertebra (.182); 1 caudal vertebra (.183).

Remarks: The beaver is found throughout most of North America except for southern peninsular Florida, the arid regions in the Southwest, and along Arctic shorelines (Kurten and Anderson 1980). The presence of this semiaquatic species in the Ardis local fauna indicates the presence of a nearby wooded, permanent body of water.

Presence in the South Carolina fossil record from Edisto Beach was first established by Roth and Laerm (1980), although they state that the single postcranial element may be modern.

Family Muridae

Subfamily Arvicolinae

Ondatra zibethicus - Muskrat

Material: 1 complete skull (.27); 2 partial skulls (1 USNM), (1 UF); 4 parietals (.28-.30), (1 USNM); both maxillaries and palate missing

only left M1 (.31); 9 right dentaries (.32-.35), (3 USNM), (2 UF); 8 left dentaries (.36-.38), (2 USNM), (3 UF); 1 left m1 (.39); 1 left m2 (.40); 1 right m2 (.41); 1 right m3 (.49); 1 left m3 (.50); 4 right M1 (.47, .48), (2 USNM); 4 left M1 (.42-.45); 1 right M3 (.46), 1 left M3 (.39); 1 left and 1 right lower incisor (.51, .52); 1 upper left incisor (.53); 12 left femora (.54-.59), (3 USNM), (3 UF); 10 right femora (.60-.63), (3 USNM), (3 UF); 9 left humeri (.64- .66), (3 USNM), (3 UF); 3 right humeri (.67- .69); 12 left tibio-fibula (.70-.75), (3 USNM), (3 UF); 13 right tibio-fibula (.76- .82), (3 USNM), (3 UF); 8 left ulna (.83-.86), (2 USNM), (2 UF); 9 right ulna (.87-.89), (3 USNM), (3 UF); 2 radii (.90- .91); 1 partial ilium (.92); 11 left partial innominates (.93- .97), (3 USNM), (3 UF); 11 right partial innominates (.98-.104), (2 USNM), (2 UF); 2 left 1st metatarsals (.105, .106); 2 left 2nd metatarsals (.121, .122); 3 left 3rd metatarsals (.115-.117); 3 right 1st metatarsals (.118- .120); 7 right 2nd metatarsals (.107- .109), (2 USNM), (2 UF); 5 right 3rd metatarsals (.110- .112), (1 USNM), (1 UF); 2 right 4th metatarsals (.113, .114); 3 calcanea (.123- .125); 1 atlas vertebra (.126); 2 axis vertebra (.127, .128); 1 3rd cervical vertebra (.129); 2 5th cervical vertebrae (.130, .131); 3 6th cervical vertebrae (.132- .133), (1 USNM); 15 caudal vertebrae (.135- .143), (3 USNM), (3 UF); 3 articulated caudal vertebrae (.134a-c); 1 lumbar vertebra (.144); 1 thoracic vertebra (.145); 9 vertebrae (.146- .148), (3 USNM), (3 UF); 1 vertebra (.150); 1 sacral vertebra (1 USNM); 1 sacral vertebra and two associated caudal vertebra (1 UF); 1 partial hyoid process (.149); 2 proximal rib halves (.151, .152).

Remarks: The muskrat is by far the most common mammal from the Ardis local fauna. The relatively high number of muskrat remains from the site suggests that they may have been using the solution cavities as temporary shelters. Given that the deposit at the Ardis local fauna represents fluvial episodic events, these cavities may have provided excellent temporary shelters if muskrats retreated from their usual shelters onto higher ground during periodic flooding. This behavior has been observed in muskrats using multiple shelters in areas with seasonal fluctuations in water levels (Brooks 1985). In addition, pieces of fossil turtle shell collected from the site had gnaw marks of a large rodent, presumably muskrats, suggesting that feeding may have occurred in these cavities. It is unlikely that the turtle shells were "wash-ins," as no signs of weathering, water wear, or abrasive breakage were evident. There have been many reports of contemporary muskrats feeding upon turtles (Errington 1941, Doult et al. 1966, Parmalee 1989), but no reports of this have been recorded from the fossil record.

The muskrat is found throughout much of North America, including all of South Carolina. This is the most aquatic of the microtine rodents and is usually found in close proximity to fresh or brackish waters.

This is the first fossil record of this species from South Carolina.

Neofiber alleni - Round-tailed Muskrat (Florida Water Rat)

Material: 1 right M1 (.153); 1 fragmentary molar (.154).

Remarks: *N. alleni* is endemic to Florida and southernmost Georgia, and its northward limits may be maintained by aridity and cold temperatures (Frazier 1977). It is not currently sympatric with *O. zibethicus*.

The enamel above the jaw line on the partial molar appears to be chemically etched or corroded. This may be due to the ingestion of this specimen by a carnivore, at which point only the dorsal portion of the tooth would be exposed to stomach acids (Gary Morgan, Florida Museum of Natural History, personal communications). Separation of the molar from the dentary bone may have occurred during or after fossilization. This species is a good indicator of nearby bodies of permanent water; its diet consists mostly of aquatic vegetation. It builds its nest in areas such as open savannahs, mangroves, and in suitable stumps (Kurten and Anderson 1980).

This is the first fossil record of the round-tailed muskrat outside of Florida and Georgia.

Synaptomys cooperi - Southern Bog Lemming

Material: 1 right M1 (.155).

Remarks: The molar from the Ardis site compares favorably to recent specimens of this species. Separation of *Synaptomys cooperi* from *S. australis* is based on size, as *S. cooperi* is generally 35% smaller than *S. australis* (Simpson 1928, Olsen 1958). The occlusal length (2.2 mm) of the Ardis M1 referred to *S. cooperi* is comparable to the lowest range given by Guilday et al. (1977).

The southern bog lemming can be found in habitats that include grasslands, moist meadows, woodlands, thickets, weedy fields, and bogs (Webster et al. 1985).

Synaptomys cooperi does not occur in the State today; the nearest populations are found in the Piedmont and mountains of Virginia and North Carolina, respectively, extending north into Maryland, and westward into Kansas and Nebraska (Hall 1981). *S. cooperi* also occurs in the Great Dismal swamp and on the Coastal Plain of North Carolina (Clark et al. 1993).

This is the first fossil record of the southern bog lemming from South Carolina.

Synaptomys australis - Florida Bog Lemming

Material: 1 right M1 (.156).

Remarks: This species, though morphologically similar to *S. cooperi*, was distinguished by its significantly larger occlusal surface length of 3.4 mm than *S. cooperi* (Simpson 1928, Olsen 1958). Apparently this is the first sympatric occurrence of *S. cooperi* and *S. australis* in a fauna known to be contemporaneous. Both species were recovered from Ladds quarry, Georgia, but may have come from strata of two different ages in the deposit (Kurten and Anderson 1980).

There has been some debate over whether or not the extinct *S. australis* is a full species, represents a cline for greater body size, or a large subspecies of *S. cooperi*. Their sympatric occurrence in the Ardis Local Fauna suggests that they were distinct.

This is the first fossil record of this species from South Carolina.

Microtus pennsylvanicus - Meadow Vole

Material: 2 right dentaries one complete (.158) and the other containing only the m1 (.159); 2 left dentaries, one missing its proximal third and the m3 (1 USNM), and one fragment containing only the m1 (.160); 2 palatines, one with right M1 and M2 along with zygomatic arch (.161) and one with right M1 and the left M2 (.162).

Remarks: The meadow vole today inhabits a wide variety of habitats including upland grasslands, meadows, swamps, stream borders, salt marshes, and forests (Webster et al. 1985).

M. pennsylvanicus is commonly collected from Pleistocene sites in North America (Kurten and Anderson 1980), and now occurs in the Piedmont and in isolated populations near Charleston, South Carolina, and Cedar Key, Florida (Webster et al. 1985, Woods et al. 1982). *M. pennsylvanicus* does not currently occur in the vicinity of the Ardis fauna.

This is the first fossil record of this species from South Carolina.

Microtus pinetorum - Woodland Vole

Material: 1 right dentary with a complete dentition (.163); 1 right m1 (.164); 2 left dentaries, one missing proximal third and m3 (.165), one missing proximal third and m2 and m3 (.166); 1 maxilla with left M1 and the right M3 (.167).

Remarks: Identification was based on criteria established by Martin and Webb (1974) and Martin (1991). The woodland vole typically

inhabits woodland and old-field habitats and is well known for building extensive shallow tunnels (Webster et al. 1985). *M. pinetorum* can be found throughout South Carolina and is common in the pine forests of the South and in eastern deciduous forests (Kurten and Anderson 1980).

This is the first fossil record of this species from South Carolina.

Subfamily Sigmodontinae

Oryzomys palustris. - Marsh Rice Rat

Material: 1 left dentary lacking dentition (.175).

Remarks: Identification was based on several features, including double rooted molars, mental foramen at base of M1, diastema short and robust (compared to *Peromyscus*), anterior root of M1 ventral and offset from other roots, foramen next to M3 much larger than *Peromyscus*, and over-all size correlation to *Oryzomys*, and direct comparisons to recent specimens.

The marsh rice rat inhabits marshlands, meadows, and wet grasslands on the Coastal Plain of South Carolina and has been recorded along a mountain stream in South Carolina (Webster et al. 1985).

This specimen represents the first fossil record of this species from the State.

Peromyscus sp.

Material: 1 right dentary containing only the incisor (.168).

Remarks: Identification was based on the alveolar length of the tooth row, and similarities in morphology and size when compared to recent *Peromyscus*. The tooth row is longer than that of *Reithrodontomys*.

Several species of *Peromyscus* inhabit the northwestern portion of South Carolina. *P. gossypinus*, the largest member of this genus inhabiting the State, is the only species of *Peromyscus* that can be found today in the area of the Ardis site. The robustness of the fossil specimen suggests this species, but, given the presence of numerous extralimital species in the fauna, it is not possible to assign the fossil to a particular species of *Peromyscus* with any certainty.

Neotoma floridana - Eastern Woodrat

Material: 1 left M1 (.169); 1 right innominate bone (.170).

Remarks: Woodrats are notorious collectors of natural history objects. Apparent rarity of this species in the Ardis local fauna notwith-

standing, activities of this species may explain some of the more unusual occurrences of other vertebrate species in the solution cavities. The three-rooted M1 compares favorably in morphology and size (anterior-posterior length of M1 = 3.52 mm) to recent material. *N. floridana* is the only species of woodrat found in the southeastern United States.

This represents the first fossil record of this species from South Carolina.

Family Hydrochaeridae

Material: 1 fragment of the posterior lamina of the M3 (.184).

Remarks: Identification to family was based on direct comparison to fossil and recent specimens. However, the fragmentary nature of the specimen precludes identification to genus or species.

The extremely thin enamel and the particular angle of the fragment are diagnostic and cannot belong to any other taxon.

One living genus of capybara (*Hydrochaeris*) occurs in tropical habitats in Central and South America and is semiaquatic, commonly found along the edges of streams and the borders of marshes (Kurten and Anderson 1980). The presence of this tropical family in the fossil record was first established for South Carolina by Roth and Laerm (1980).

Order Lagomorpha

Family Leporidae

Sylvilagus palustris - Marsh Rabbit

Material: 4 right dentaries (.185-.187), (1 UF); 3 left dentaries (.188-.189), (1 USNM); 1 isolated p3 (.190).

Remarks: Identification was based on the presence of multiple anterior reentrants on the third premolar.

The marsh rabbit is a good swimmer and can be found in wetlands areas such as marshes, flood plains, and hummocks, and its modern distribution ranges from southeastern Virginia along the Atlantic Coastal Plain into Florida (Webster et al. 1985). *S. palustris* probably occurs in the immediate vicinity of the Ardis site. It has been recorded from many Pleistocene sites in Florida (Webb 1974, Kurten and Anderson 1980), and *Sylvilagus* sp. was identified from Edisto Island, South Carolina (Roth and Laerm 1980).

This represents the first fossil material identified as this species from South Carolina.

Sylvilagus floridanus - Eastern Cottontail

Material: 2 left (.191, .192) and 1 right dentary (1 USNM).

Remarks: Remains were identified by complete absence or presence of a single anterior reentrant on the p3.

This species is distributed from southern Canada south to Argentina (Kurten and Anderson 1980). The eastern cottontail typically inhabits areas with a mixture of herbaceous and shrubby plants in a disturbed environment at some stage of successional transition that occur in and among a variety of habitats (Webster et al. 1985). The eastern cottontail occurs in the area of the Ardis site today.

This is the first fossil record of this species reported from South Carolina.

Sylvilagus sp.

Material: 2 right distal femora fragments (.213, .214); 3 left partial femora (.215, .216), (USNM); 1 right humerus (.217); 1 left distal half of a humerus (.218); 1 proximal end of a humerus (.226); 1 right partial scapula (.219); 2 distal and 1 proximal tibio-fibia ends (3 USNM); 1 left partial radius (.220); 1 ulna proximal end (.221); 4 left partial innominate bones (.222, .223), (2 USNM); 3 left calcanea (.224), (2 UF); 3 right calcanea (.225), (2 USNM).

Remarks: All of the leporid postcranial elements from the Ardis local fauna represent this genus, but we are unable to assign these elements to a particular species in this genus.

DISCUSSION

PALEOECOLOGY AND PALEOCLIMATE

The Ardis local fauna is one of only a handful of Rancholabrean sites reported from the Atlantic Coastal Plain north of Florida, and is the only C14 dated fauna from South Carolina. It was deposited during the full glacial phase of the Wisconsin. This interval is poorly represented in the fossil record, with New Trout Cave, West Virginia (Grady and Garton 1982) and Bakers Bluff, Tennessee (Guilday et al. 1978) being the only other fossil sites in the southeastern United States known to be temporally similar.

Two biases must be considered which may have skewed types and frequency of remains recovered from the Ardis site: 1) collection bias; a disproportional amount of the larger "easier to see" material was collected. Comparatively little of the fossiliferous sediments was screen-washed to retrieve the smaller material otherwise easily missed

and 2) depositional and behavioral biases; the smaller taxa, particularly those that used this site as a shelter or in hunting, should be represented in disproportionately higher numbers when compared to the megafauna. Behavioral and environmental factors influence the occurrence of the smaller taxa which could easily enter the cavities from the surface. Furthermore, some taxa may have been concentrated in the stomachs of predators who were subsequently entombed in the cavities. The above-mentioned factors, excluding predation, but including other taphonomic factors, especially the size-restrictive nature of the cavity openings, would govern the lower frequency of the larger megafauna occurrence in the cavities. Therefore, the species composition most likely is not proportional to its true occurrence in this particular Pleistocene community.

Relatively large faunal diversity may give a reasonably reliable picture of the surrounding habitat (Guilday 1962). The taxa of the Ardis local fauna represent a diversity of ecological niches including semi-aquatic forms (*Castor*, *Lontra*, *Ondatra*, *Tapirus*, and *Mustela vison*), arboreal forms (*Glaucomys volans*, *Sciurus carolinensis*), marsh and meadow inhabitants (*Synaptomys*, *Microtus*, *Oryzomys*), grassland or prairie forest transition inhabitant (*Spermophilus tridecemlineatus*), and the large grazers and browsers (*Palaeolama*, *Bison*, *Equus*, *Odocoileus*, *Megalonyx*, *Mammut*, and *Mammuthus*), suggesting that the Ardis fauna sampled an ecological mosaic of community types. The depositional features and fauna suggest a composite conifer and hardwood forest, interspersed or bordered by a grassland/meadow, possibly giving way in low-lying areas to a marsh or bog, with a permanent nearby stream or river.

Hypothesized changes in vegetation during the late Pleistocene (Dreimanis 1968), with climatic conditions unlike any experienced in North America today (COHMAP Members 1988), are reflected in the extralimital tropical to boreal species found in the Ardis fauna.

Of the 43 mammalian species collected from the site, 27 are extant, 21 still occurring in the area today. Of the six extant extralimital taxa, four have more northern affinities, one a midwestern affinity, whereas only one has a range well south of the Ardis site. Of the 16 extinct taxa, five have affinities considerably south and west of the Ardis locality (Kurten and Anderson 1980, Martin 1978).

The Ardis mammal fauna exhibits a mixture of southern, western, and northern forms, resulting from the radiation and convergence onto the lower Atlantic Coastal Plain of taxa migrating along the Gulf Coast corridor (Webb 1974) and taxa migrating from the north-west Appalachian Mountains region. It is plausible that *Spermophilus tridecemlineatus* may have entered South Carolina from a northern

route instead of along the Gulf Coast corridor, as attributed to the fossil remains from the Haile 14A fauna (Webb 1974). Fossil localities reporting *S. tridecemlineatus* (Kurten and Anderson 1980) and other fossils collected from the Ardis site, in particular a portion of the turtle fauna (Bentley and Knight, submitted), strongly suggests the existence of a northern corridor(s) onto the Atlantic Coastal Plain. This would be a logical pathway for those glacially displaced species of the Northeast found at the Ardis site.

Blarina brevicauda, *Microtus pennsylvanicus*, and *Synaptomys cooperi* are interpreted as "boreal" or "cool climate" components of the Ardis fauna, based on modern distribution and habitat orientation (Hoffman and Jones 1970, Graham 1976, Webster et al. 1985). *Neofiber alleni* is considered a sub-tropical or "warm climate" species based on modern distribution and fossil records (Martin and Webb 1974, Frazier 1977, Kurten and Anderson 1980, Holman 1985).

Those extinct species collected from the Ardis fauna with extant genera or families primarily tropical to sub-tropical in distribution include: *Tremarctos floridanus*, *Palaeolama mirifica*, *Conepatus robustus*, *Tapirus veroensis*, and the family Hydrochoeridae. *Holmesina septentrionalis* has also been interpreted as indicating a mild climate (Kurten and Anderson 1980).

Generalization of ecological needs of an extinct species based on the needs of extant relatives cannot always be considered reliable. However, when several such groups are geologically recent, are in a single locality, and represent a short depositional time interval, as at the Ardis site, these assumptions become more credible.

The modern Coastal Plain fauna of South Carolina has six species of microtines, three species of shrews, and two mole species (Webster et al. 1985). Fossil remains of both mole species and two of the three shrew species were collected from the Ardis fauna, along with eight microtine species. Greater microtine densities in late Pleistocene faunas have been correlated with reduced temperature and moisture gradients (Graham 1976). This is also true for shrew species (Graham 1976), but we did not observe it in the Ardis fauna. The reduction in the number of shrew species at the Ardis site is probably a result of collection bias and not a true reflection of the shrew populations.

Martin (1968) suggested that the distribution of *M. pennsylvanicus* is limited mostly by warmer temperatures and drier summers, but also by the presence of *Sigmodon hispidus*, which was inexplicably absent from the Ardis fauna. The mean July temperature for the southern boundary of *M. pennsylvanicus* is 23.9 ± 1.1 C (Martin 1968), and

the two species occur sympatrically in areas where the mean July temperature is near 26.7 C (Martin 1968). Today, *S. hispidus* is common throughout South Carolina, but *M. pennsylvanicus* is present only in the extreme western Piedmont and in a small relict population near Charleston, South Carolina (Webster et al. 1985). Data from Charleston, South Carolina, over the past 75 years yielded a July daytime mean of 31.1 C and a minimum daily mean of 23.9 C (Pearce and Smith 1984). Vegetational data for the late Wisconsin full glaciation, taken from White Pond in South Carolina (Watts 1980), suggested a 7 C to 20 C decrease in July temperatures compared to present, and possibly a marginal reduction in precipitation. The presence of *M. pennsylvanicus* in the Ardis fauna and the absence of *S. hispidus* may indicate slightly drier conditions and temperatures below the mean summer temperature experienced today.

It has been postulated that mammals in the late Pleistocene reacted to environmental changes based on their own tolerance limits and not as a "community unit" (Graham 1976, 1979). This accounts for northern species pushed south by glaciation and then integrating with the existing biota. Furthermore, southern species also were integrated into the resident community as cooler summers and warmer winters prevailed, producing the "disharmonious fauna" collected from the Ardis fauna.

In general, the mammalian composition of the Ardis fauna, containing distinctly southern, northern, and western extralimital forms, reflects a climate more equitable than present. The less severe climatic gradients would facilitate the sympatric occurrence of species now ecologically incompatible. The Ardis local fauna coincides well with other late Pleistocene fossil localities reporting disharmonious faunas with similar temporal and topographical settings. This suggests that the late Pleistocene in the southeastern United States was climatically more equitable and ecologically more diverse prior to the dramatic shift towards a modern assemblage, approximately 10,000 to 11,000 y.b.p. (Lundelius et al. 1983).

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APPENDIX I

TAXA AND MINIMUM NUMBER OF INDIVIDUALS

Taxa	Minimum Number of Individuals
<i>Didelphis virginiana</i> *	6
† <i>Dasypus bellus</i>	1
† <i>Holmesina septentrionalis</i> (S)	1
† <i>Megalonyx jeffersoni</i>	1
<i>Sorex</i> sp. cf. <i>S. longirostris</i> *	1
<i>Blarina brevicauda</i> *(N)	3
<i>Scalopus aquaticus</i> *	11
<i>Condylura cristata</i> *	2
<i>Urocyon</i> cf. <i>U. cinereoargenteus</i>	1

† <i>Canis dirus</i>	1
†cf. <i>Smilodon fatalis</i>	1
<i>Lynx rufus</i> *	1
<i>Lontra canadensis</i> *	1
<i>Spilogale putorius</i> *(N)	1
<i>Mephitis mephitis</i> *	1
† <i>Conepatus robustus</i> *(S)	1
<i>Mustela vison</i> *	5
<i>Procyon lotor</i>	2
† <i>Tremarctos floridanus</i> (S)	1
† <i>Mammut americanum</i>	1
† <i>Mammuthus columbi</i>	2
† <i>Equus</i> cf. <i>E. complicatus</i>	2
† <i>Tapirus veroensis</i>	2
† <i>Mylohyus nasutus</i>	1
† <i>Palaeolama mirifica</i> (S)	1
<i>Odocoileus virginianus</i>	2
† <i>Bison antiquus</i>	1
<i>Glaucornis volans</i> *	1
<i>Sciurus carolinensis</i> *	1
<i>Spermophilus tridecemlineatus</i> *(MW)	1
<i>Castor canadensis</i>	1
<i>Ondatra zibethicus</i> *	13
<i>Neofiber alleni</i> *(S)	1
<i>Synaptomys cooperi</i> *(N)	1
† <i>Synaptomys australis</i> *(S)	1
<i>Microtus pennsylvanicus</i> *(N)	3
<i>Microtus pinetorum</i> *	3
<i>Oryzomys palustris</i> *	1
<i>Peromyscus</i> sp.*	1
<i>Neotoma floridana</i> *	1
Hydrochoeridae(S)	1
<i>Sylvilagus palustris</i> *	4
<i>Sylvilagus floridanus</i> *	2
Faunal list = 43 species	Total 89

* = first fossil record from South Carolina

(N) = extralimital northern (S) = extralimital southern

(MW) = extralimital mid-western

† = Extinct taxa

Comments on the Body Mass Trend
of *Ondatra zibethicus* (Rodentia: Muridae)
During the Latest Pleistocene

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ABSTRACT—Martin (1993) suggested, in his investigation of the phyletic evolution in the rodent genus *Ondatra*, that an increase in body mass through time has occurred in *Ondatra zibethicus*, with the increase in size being concentrated in the last 600,000 years before present (y.b.p.). *Ondatra zibethicus* apparently obtained its greatest body mass during the latest Pleistocene, followed by a sharp decrease in body mass into Recent times, referred to as a "dwarfing event." We examined fossil muskrats from late Pleistocene sites in South Carolina, Florida, and additional Recent material which do not support the proposed "dwarfing event" of *O. zibethicus* at the close of the Pleistocene. As more fossil material becomes available, future research could provide a clearer picture of the body mass trend in *Ondatra zibethicus*.

METHODS

Two recently discovered late Pleistocene sites, Crowfield local fauna and the Ardis local fauna (Bentley et al. 1994) yielded fossils of *Ondatra zibethicus*. These remains, coupled with unpublished material from the Aucilla River, Florida, and Recent specimens from Iowa and Georgia provided new data elucidating body mass trend for this taxon during the latest Pleistocene. It is not within the scope of this paper to do a thorough review of the literature on muskrat body mass nor extensive studies of museum collections. A project of this magnitude would encompass an undertaking much larger than this note. The data published here are intended to elicit further research into the trends of muskrat body mass at the close of the Pleistocene.

Boyce (1978) noted a small degree of sexual dimorphism in muskrats with males slightly larger than females. However, because this difference is slight, and sex cannot be determined from fragmentary fossil material, the effects of sexual dimorphism can not be assessed in this study.

All measurements were done on the first lower molar (m1). Measurements were taken three times with calipers and rounded to the nearest 0.01 mm.

Fossil specimens from the Ardis local fauna, deposited in the collections of the South Carolina State Museum (SCSM), are designated by the base number S. C. 93.105. and cited in this paper by the two digits following the base number. Specimens from the Crowfield local fauna and Recent unaccessioned specimens at the South Carolina State Museum are denoted by SCSM. Fossil material from the Florida Museum of Natural History is indicated by the accession numbers of 132680 - 131318.

We used a weighted, Wilcoxon rank analysis test to search for statistical significance between our data and Martin's. The data were analyzed over three time intervals: 1) 20,000 y.b.p. to Recent; 2) 20,000 y.b.p. to 10,000 y.b.p.; 3) 20,000 y.b.p. to 15,000 y.b.p. The Wilcoxon rank analysis test was used to compare sample means, as Martin's raw data were not available to us.

INTRODUCTION

Martin (1993) derived a regression formula based on the length of the ml to estimate the body mass of arvicolines: $M = 0.71 (L)^{3.59}$, where M is body mass in kg and L is the length of ml in mm. He used the formula to help determine the trend in body mass for the polytypic genus *Ondatra* during the last 3.75 million years. Martin noted that most of the change in body mass occurred during the last 600,000 years. Muskrats reached their greatest size (1.75 kg) during the latest Wisconsin between 20,000 and 10,000 y.b.p. This larger form was *Ondatra zibethicus floridanus* (Lawrence 1942), synonymized with *O. zibethicus* by Martin (1993). Martin conjectured that approximately 10,000 years ago it appears that body mass dramatically decreased to the levels he recorded for Recent samples. Martin referred to this decline in body mass as a "dwarfing event." He was unclear as to the cause but mentioned human culling and/or natural selection as possible explanations. Applying Martin's regression formula to fossils from several recently collected late Pleistocene sites in South Carolina and Florida, as well as recent specimens from Iowa and Georgia (Table 1), gives more resolution to this short, but apparently dynamic time interval.

RESULTS AND DISCUSSION

The Ardis local fauna (19,000 y.b.p.) (Bentley et al. 1994) yielded 18 *Ondatra* ml's for which measurements could be taken (Table 1), producing a mean body mass of 0.95 kg. An unpublished fauna from South Carolina, the Crowfield local fauna (80,000 y.b.p.),

under study by Fred Grady of the National Museum of Natural History, produced a sample of six muskrat ml's giving a mean of 0.92 kg. In Florida, an unpublished, late Pleistocene site (12,000–10,000 y.b.p.), from the Aucilla River (Priscilla site, Little River section), under study by S. David Webb (Florida Museum of Natural History, personal communication), yielded 15 ml's with a mean of 1.04 kg. The age of this site is based on numerous radiocarbon dates (Dunbar et al. 1989; S. D. Webb, personal communication).

The senior author obtained 22 muskrat carcasses from a fur buyer in Roselle, Carroll County, Iowa, in December 1992. The sample represents muskrats from populations within a 100-mile radius of Roselle and were probably collected from many different sites. Using Martin's regression formula, these samples produced a mean of 0.94 kg. Measurements of two modern ml's from Georgia (no other data) had estimated mean mass of 1.27 kg.

Comparing these data (Fig. 1) with those of Martin (unpublished data) would suggest that the increase in body mass for the time span covered by our samples was much more subtle than Martin's data would indicate. After Martin's initial body mass increase at 600,000 y.b.p., the upward change in size until Recent is almost negligible. In addition, the statistical analysis of the three time intervals yielded no significant difference between our data and Martin's. Thus, our data do not support Martin's "dwarfing event" at the close of the Pleistocene.

We view the data on which the dwarfing hypothesis was based as having several problems, the most significant of which is sample size. The four samples between 10,000 and 20,000 y.b.p. which constitute the much larger forms of *O. zibethicus* (compared to Recent specimens) are made up of a total of seven ml's, from four sites (Table 2), an extremely small sample size. Furthermore, all of Martin's 10,000–20,000 y.b.p. specimens were recovered from cave faunas (Table 2), a habitat in which modern muskrat populations do not naturally occur. This would suggest that various selection pressures, probably predatory, must be taking place in order for these remains to occur in cave deposits. Thus, the samples from these caves may not be a true representation of nearby local populations.

Assuming that Martin's regression for body mass holds true, it seems highly probable that a "dwarfing event" has not occurred between the latest Pleistocene and contemporary times based on this new material. However, this has little consequence for the overall trend in muskrat body mass over the past 3.75 million years. When this time period is re-scaled to a common interval length, Martin (1993) states that the dwarfing event "... appears to be only moderately pronounced."

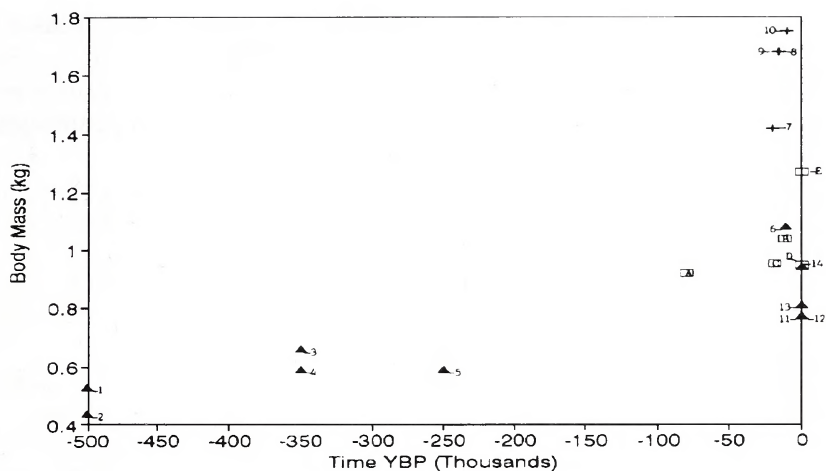


Fig. 1. Mean body mass trend of *Ondatra zibethicus*. Solid triangles: sample means for non-cave faunas reported by Martin (1993). Plus symbols: sample means for cave faunas reported by Martin (1993). Open squares: sample means for non-cave faunas (from Table 1). Overlapping samples are denoted by two location numbers. Numbers and letters indicate location of the samples (from Table 2).

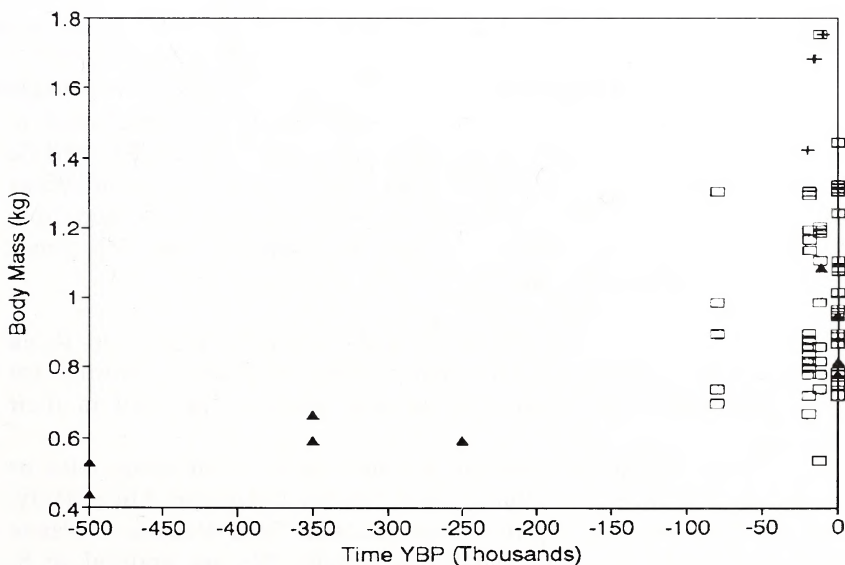


Fig. 2. Comparison of raw versus mean data points for *Ondatra zibethicus*. Solid triangles and plus symbols are Martins' (1993) sample means. Open squares are Bentley and Knight's raw data (from Table 1).

Table 2. Location, sample size, and age of muskrat specimens.

Locality	Sample Size	Age (y.b.p.)	Source	
1-Mulen 3	6	500,000	Martin	(unpublished)
2-Kanopolis	1	500,000	"	"
3-Hay Springs	7	350,000	"	"
4-Anderson/Flohr	2	350,000	"	"
5-Doby Springs	11	250,000	"	"
6-Ichetucknee River	23	11,000	"	"
7-Bell Cave Z3	3	20,000	"	"
8-Bell Cave 1/2	1	15,000	"	"
9-Yarbrough Cave	2	16,000	"	"
10-Kingston Cave	1	10,000	"	"
11-Louisiana	31	Recent	"	"
12-Br. Columbia	10	Recent	"	"
13-Nebraska	10	Recent	"	"
14-New Jersey	17	Recent	"	"
A-Crawfield	5	80,000	Bentley & Knight (Table 1)	
B-Aucilla River	15	12-10,000	"	"
C-Ardis L.F.	18	19,000	"	"
D-Iowa	22	Recent	"	"
E-Georgia	2	Recent	"	"

We believe the "dwarfing event" is an artifact of small sample sizes and selection bias and not a dramatic evolutionary response to some environmental change. However, further data are needed to provide a more definitive answer to the true body mass trend of *Ondatra zibethicus* during the latest Pleistocene. As fossil collections are amassed from the latest Pleistocene a clearer picture may develop, resolving trends that cannot be discerned here.

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Introductions of the Scorpions *Centruroides vittatus* (Say) and *C. hentzi* (Banks) into North Carolina, with
Records of the Indigenous Scorpion,
Vaejovis carolinianus (Beauvois)
(Scorpionida: Buthidae, Vaejovidae)

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ABSTRACT—The scorpions *Centruroides vittatus* (Say) and *C. hentzi* (Banks), with subaculear tubercles on their telsons, have been accidentally imported into piedmont and coastal North Carolina and may become established in parts of these regions. They are distinguished by the larger size of *C. vittatus* and by the following differences in pigmentation: the presence of a darkly pigmented, inverted triangular patch on the cephalothorax of *C. vittatus*, as opposed to light mottled brownish coloration in *C. hentzi*, and by the reticulated brown pigmentation on the dorsal surfaces of the chelicerae of *C. hentzi*, in contrast to the unpigmented condition in *C. vittatus*. The native scorpion, *Vaejovis carolinianus* (Beauvois), which lacks the subaculear tubercle, occurs in southwestern border counties adjoining South Carolina and Georgia and has penetrated the western fringe of the State, occurring just inside the Tennessee state line in the French Broad and Little Tennessee river valleys. It is also recorded from Yancey, Haywood, Mecklenburg, Iredell, Guilford, Wake, and Columbus counties, all probably representing accidental human importations. A key, descriptive drawings, and a map of occurrences are presented.

In April 1991, I was notified that employees in a north Raleigh office building had encountered and trapped a scorpion in a hallway. *Vaejovis*¹ *carolinianus* (Beauvois) (family Vaejovidae), occurring in southwestern border counties adjoining South Carolina and Georgia, some 208 mi (333 km) from Raleigh (Shelley 1975a, b), is the only scorpion native to North Carolina, so I was surprised to find that they had a specimen of *Centruroides vittatus* (Say) (family Buthidae), a species occurring in the southcentral and southwestern United States and the adjacent states in northern Mexico (Stahnke and Calos 1977). This individual had been unknowingly transported to North Carolina in a shipment of mesquite lumber for an adjoining

¹ Francke (1977) showed that *Vaejovis* and Vaejovidae, with an "a", are the correct spellings for the genus and family, respectively, as opposed to the previous orthography without this vowel.

steak restaurant and had wandered into the office building. Occupants reported seeing occasional scorpions for a year previously, but thorough searches of the building, its grounds, and a nearby rocky ditch in both daytime and at night, using a black light, produced no more specimens. Shortly afterwards I learned that individuals of *C. vittatus* had been encountered near downtown Raleigh and in a building in the Research Triangle Park, in both cases near restaurants using mesquite to broil steaks. The species has also been collected in Nash and Dare counties, and a Florida scorpion, *C. hentzi* (Banks), has been discovered in Carteret and Brunswick counties, on the North Carolina coast, and in Durham County in the Piedmont. Thus, three scorpions (dorsal views in Fig. 1) may now be encountered in North Carolina.

The origins of most accidental animal introductions cannot be traced, but if reproducing populations of either *C. vittatus* or *C. hentzi* become established in North Carolina through the introduction of a gravid female or a mating pair, I believe they will have resulted from

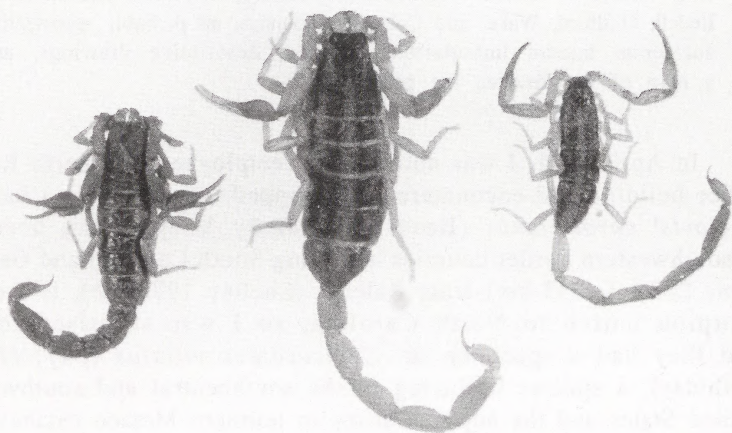


Fig. 1. Dorsal views of, left to right, *V. carolinianus*, *C. vittatus*, and *C. hentzi*.

human introductions that occurred primarily in the late 1980's and the early 1990's. Both species can potentially survive and reproduce in parts of North Carolina, thereby becoming components of the State's fauna. Likewise, *V. carolinianus* can potentially survive and reproduce north and east of Polk, and the adjacent fringe of Rutherford, counties. If such populations are ever discovered, they too will date from the late 1980s and early 1990s.

These scorpions are not dangerous to man, their stings being roughly comparable to those of bees and wasps. Muma (1967) reported that the sting of *C. hentzi* produced a localized burning sensation and that the area was tender for a few hours; the venom of *C. vittatus* produces a similar, though more painful, reaction. No information is available on the venom of *V. carolinianus*, but no species of this genus is known to be harmful (Muma 1967).

For the benefit of local naturalists, I announce the discovery of these non-native arachnids in North Carolina, publish the available records along with an identification key and pertinent illustrations, and update the known localities of *V. carolinianus*. Acronyms of sources of preserved study material are as follows:

AMNH - American Museum of Natural History, New York,
New York.

DEH - Division of Environmental Health, Public Health Pest
Management Section, North Carolina Department of
Environment, Health, and Natural Resources, Raleigh.

FMNH - Field Museum of Natural History, Chicago, Illinois.

FSCA - Florida State Collection of Arthropods, Gainesville.

MEM - Mississippi Entomological Museum, Mississippi State
University, Starkville.

MMNS - Mississippi Museum of Natural Science, Jackson.

NCDA - Division of Plant Industry, North Carolina Department
of Agriculture, Raleigh.

NCSM - North Carolina State Museum of Natural Sciences, Raleigh.

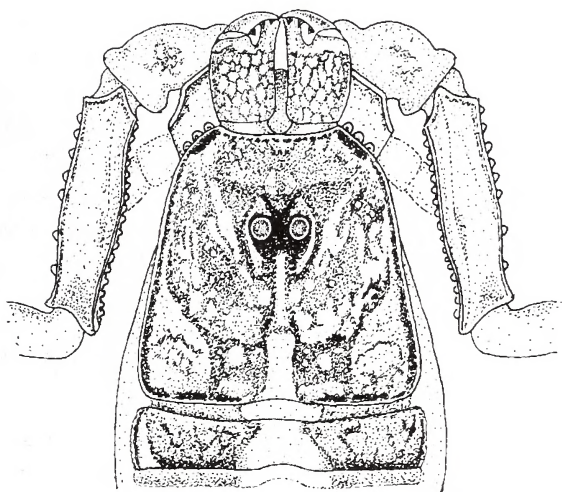
NCSU - Entomology Department, North Carolina State University,
Raleigh.

NMNH - National Museum of Natural History, Smithsonian
Institution, Washington, DC.

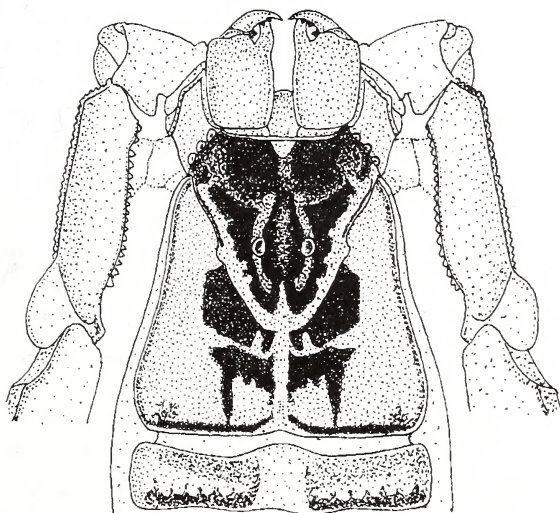
NSC - Natural Science Center, Greensboro, North Carolina.

RNH - Private collection of R. N. Henson, Boone, North Carolina.

SEM - Snow Entomological Museum, University of Kansas, Lawrence.



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Figs. 4-5. Color patterns of the chelicerae and cephalothorax.
4, *C. hentzi*; 5, *C. vittatus*.

Family Buthidae

Centruroides vittatus (Say)

Habitat—In its native range, *C. vittatus* occurs in a wide variety of microhabitats in deserts, deciduous and pine forests, and grasslands. It lives in cracks and crevices of rocky outcrops and canyons walls, climbs into vegetation, occurs beneath yuccas in deserts and grasslands, and commonly enters houses (W. D. Sissom, West Texas A&M University, personal communication). The specimens from Nash and Dare counties, the Research Triangle Park, and Bland Road, Raleigh, were discovered inside buildings; those at the last two sites were walking across a room and a hallway. The specimen from Wakefield Street, Raleigh, was found by workers digging behind a building.

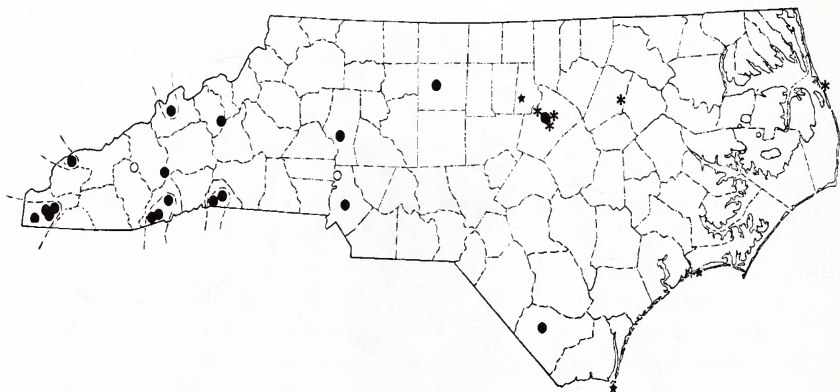


Fig. 6. Occurrences of scorpions in North Carolina. Dots, *V. carolinianus*; stars, *C. hentzi*; asterisks, *C. vittatus*. The site record from near Cowans Ford Dam, Mecklenburg County, is indicated by the eastern circle; that from Transylvania County is obscured by a dot. The western circle, in Jackson County, denotes Balsam Gap, the location from which the wood containing *V. carolinianus* in Haywood County was obtained. Dashed lines surround presumably indigenous records in western counties showing the assumed expansions from adjoining states.

Distribution—The generalized range of the southcentral and southwestern United States to northern Mexico can be stated more specifically as from Louisiana to New Mexico east of the Rio Grande and, latitudinally, from the Central Plains of the United States into the adjoining northern states of Mexico (W. D. Sissom, personal communication). North Carolina specimens were examined as follows (Fig. 6):

Wake Co., Raleigh, office building along Bland Rd., 1 spmn., April 1991, J. Wigmore (NCSM) and along Wakefield St., 1 spmn., 24 October 1986, M. A. Brittain (NCSU); and Research Triangle Park, 1 spmn., August 1991, collector unknown (NCSM). Nash Co., Rocky Mount, 1 spmn., 26 July 1991, collector unknown (NCSM). Dare Co., Nags Head, in building behind self storage facility, 1 spmn., 10 May 1986, L. Griffin (NCSU).

Remarks—Because winters in North Carolina's piedmont are considerably milder than those in its native range in the midwest, *C. vittatus* potentially could become established in the central part of the State. An introduced population now exists in Murfreesboro, Rutherford County, Tennessee (W. D. Sissom and G. A. Polis, Vanderbilt University, personal communication).

There is at least one widespread chain of restaurants that broil steaks over mesquite, so introduced, reproducing populations of *C. vittatus* may exist in major cities throughout the Southeast. Use of mesquite chips for broiling, rather than whole logs or lumber, would produce the same flavor and eliminate the possibility of importing live scorpions, not to mention unknown numbers of insects that might have an adverse economic impact on agriculture.

Centruroides hentzi (Banks)

Habitat—In Florida, *C. hentzi* is usually encountered under litter, logs, and stones; it can also be found under bark of dead trees up to 20 ft (6 m) high and commonly invades houses (Muma 1967). The Durham County specimen was discovered in a rolled towel in a dormitory; those from Carteret and Brunswick counties were found in residences in condominium buildings, the 1992 scorpion was encountered in a bathtub. At Emerald Isle, four specimens were found in hallways and closets on both floors in a beachfront Carteret County condominium complex during a two-month period in summer 1993, and two more were encountered in May 1994. Six condominium units were involved, comprising the northern half of one building; scorpions were not discovered in the other buildings of the complex. One scorpion was found dead in a man's shoe, and another stung a young child, who was

treated at Carteret General Hospital and released. A pest control operator treated inside and outside the building with pesticide but could not determine the source of the scorpions. I visited the site in October 1994 and found no specimens and little shelter near the building. The yard of the complex was immaculate, and the building is bordered by low bushes surrounded with pine straw. Some bushes had grown into relatively dense hedges, and the only external shelter of consequence was beneath these hedges. I spent two hours searching around the building, elsewhere on the complex, and in nearby wooded areas in Emerald Isle and the western tip of Bogue Banks without finding any scorpions.

Distribution—According to Muma (1967), *C. hentzi* occurs throughout Florida, occurring in Columbia County, on the border with Georgia, and in Escambia, the westernmost county. It should therefore be expected in the southern coastal islands of Georgia, where Say (1821) collected scorpions. North Carolina specimens were examined as follows (Fig. 6):

Durham Co., Durham, Duke Univ., 1 spmn., 8 September 1987, C. Brock (NCSU). *Carteret Co.*, Bogue Banks, Emerald Isle, 1 spmn., Sept. 1993, D. McCluskey (NCSM). *Brunswick Co.*, Bald Head Island, 1 mi (1.6 km) E of Marina, 1 spmn., July 1992, collector unknown (RNH) and unknown site on island, 1 spmn., February 1993, collector unknown (NCSM).

Remarks—An individual of *C. hentzi* was encountered in Raleigh on 10 March 1938 “in strawberries from Florida”; one of *C. gracilis* (Latreille) was discovered in Raleigh in the fall 1940 “in box shipped from Florida”; and an undetermined Neotropical scorpion was found in Raleigh on 13 December 1937 “in bunch of bananas from Central & South America” (all specimens in NCDA). Although not encountered in North Carolina environments, these specimens confirm that commercial activities, like importing foods and fruits from other states and foreign countries, is a key mechanism through which allochthonous organisms are accidentally introduced into distant areas. The importation of Florida palm trees for planting along the North Carolina coast can only aid the spreading of *C. hentzi* and may result in its becoming established in warm areas like Bald Head Island, where winters are not much cooler than those in northern Florida where the scorpion is common.

Family Vaejovidae

Vaejovis carolinianus (Beauvois)

Habitat—I collected *V. carolinianus* in Cherokee County from beneath large rocks on a dirt road and leaves in a deciduous forest

(Shelley 1975a), but I typically encounter the scorpion in association with decaying pine logs and stumps, particularly under loose bark. Rossman (1979) encountered specimens in clay soil on a stream bank, and beneath decaying logs, leaf litter, slabs of wood, and the bark of a dead hardwood tree. Gibbons et al. (1990) stated that *V. carolinianus* was restricted to moist woodland habitats, where it occurs beneath leaves, logs, and other litter. Several specimens from Transylvania and Polk counties were found in and around houses; that from Guilford County was taken within a house; and the one from Iredell County was discovered in a sink in the basement of a house, but it could have been imported from north Georgia, where the collector spent the previous week. The specimen from Yancey County was discovered in a tent at a campground.

Distribution—The southeastern United States from the Ohio River in central Kentucky through eastern Tennessee, southwestern North Carolina, and the Fall Zone of South Carolina and Georgia, to eastern Mississippi and westcentral Tennessee, with a disjunct population in the Tunica Hills of southwestern Mississippi and southeastern Louisiana (Rossman 1979, Gibbons et al. 1990, Shelley 1994). In North Carolina, *V. carolinianus* is native to Polk, Transylvania, and Cherokee counties, spreading into these areas and up the Toxaway and Hiwassee river valleys from adjacent parts of northern Georgia and western South Carolina. It also penetrates the western periphery by extending up the Little Tennessee and French Broad river valleys from eastern Tennessee. The scorpion also has been encountered in seven other counties, five in the interior of the State and two on the border with piedmont and coastal South Carolina, which probably represent accidental human importations and examples of intra-state introductions. The Haywood County site, in the heart of the Blue Ridge Province and at 5,000 ft. (1,500 m) elevation, the highest reported altitude for the scorpion, surely reflects an importation, as *V. carolinianus* was found in a woodpile that was brought from Balsam Gap, Jackson County. The scorpion was probably transported from the latter site (open circle in Fig. 6); Haywood County is also in the heart of the Blue Ridge and an unlikely spot for a native population. North Carolina specimens were examined as follows:

Yancey Co., Crabtree Meadows, along Blue Ridge Pkwy., 1 spmn., 8 June 1960, L. Mason (SEM). *Madison Co.*, 1 mi (1.6 km) SE Walnut, along US hwy. 25/70, 1 spmn., 25 August 1981, B. Hill (NCSM). *Haywood Co.*, Mt. Pisgah Cpgd., 1 spmn., August 1993, B. Randolph (RNH). *Swain Co.*, 0.5 mi (0.8 km) N Tapoco, along Little Tenn. R., 2 spmns., 13 August 1985, R. Gaul, J. Whitcomb, D. Anthony, R. Lee

(NCSM). *Cherokee Co.*, locality unknown, 2 spmns., J. Gallatin (NMNH) and 1 spmn., 19 June 1988, collector unknown (DEH); 6 mi (9.6 km) WNW Culberson, along co. rd. 1107, 0.2 mi (0.3 km) N jct. co. rd. 1108, 1 spmn., 27 June 1974, R. M. Shelley (NCSM); 5 mi (8 km) W Murphy, along US hwy. 64, 1 spmn., 1 October 1987, F. Bailey (RNH); 7.2 mi (11.5 km) NW Murphy, along co. rd. 1326, 0.3 mi (0.5 km) W jct. co. rd. 1406, 2 spmns., 27 June 1974, R. M. Shelley (NCSM); and 1.7 mi (2.7 km) N Murphy, 1 spmn., 22 June 1984, A. L. & A. B. Braswell (NCSM). *Transylvania Co.*, 4.5 mi (7.2 km) SW Rosman, along co. rd. 1139, 1 spmn., 3 December 1980, A. Burdo (NCSM); Brevard, 1 spmn., 5 September 1975, D. Sizemore (NCSM) and in house, 1 spmn., 18 November 1985, M. Albertson (NCSU); and along Bearcamp Cr., 0.5 mi (0.8 km) N SC border, 1 spmn., 25 June 1962, R. C. Graves (NCSM). *Polk Co.*, nr. Tryon, 1 spmn., 16 September 1934, collector unknown (NMNH); Tryon, around houses under construction, 2 spmns., 10 April 1957, D. F. Ashton (NCSM) and in leaf litter, 1 spmn., 21 November 1949, L. Eisenach (FMNH); in house 1.5 mi (2.4 km) WNW Columbus, along co. rd. 1135, 4 spmns., 21 September 1984, O. R. Ammons (NCSU); and Columbus, 3 spmns. 22 April 1957, G. D. Jones (NCSM, NMNH) and 1 spmn., 1973, P. Culberson (NCSM). *Mecklenburg Co.*, Charlotte, Farmingdale Dr., 1 spmn., 8 August 1970, M. Overton (NCSM). *Iredell Co.*, 5 mi (8 km) SSW Troutman, SR 1401 at Lake Norman, 1 spmn., 25 June 1990, K. Troutman (NCSU). *Guilford Co.*, Greensboro, 1 spmn., November 1992, collector unknown (NSC). *Wake Co.*, Raleigh, Fairway Ridge Dr., 1 spmn., 25 August 1990, F. Starnes (NCSM). *Columbus Co.*, Whiteville, 1 spmn., 9 July 1976, J. Rogers (NCSM).

The following site records are also considered valid but not substantiated by specimens:

Transylvania Co., Toxaway Gorge, under bark of logs in 1963 (J. R. Paul).

Mecklenburg Co., Cowans Ford Dam at Lake Norman, under mat in a building ca. 1987 (K. L. Manuel).

There are also two specimens taken in the "western part of state," exact location unknown, 5 October 1965, J. Gallion (AMNH).

Remarks—Because of the abundance of predominantly pine forests like those in which it occurs in piedmont South Carolina and Georgia, *V. carolinianus* could become established in central North Carolina through accidental importations from its natural range in this or other states.

ACKNOWLEDGMENTS—I thank the following curators, collection managers, and university faculty for records from their collections or loans from, and access to, specimens under their care: B. R. Engber

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Distribution of the Scorpion,
Vaejovis carolinianus (Beauvois) — a Reevaluation,
(Arachnida: Scorpionida: Vaejovidae)

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ABSTRACT—*Vaejovis carolinianus* (Beauvois) is primarily an upland scorpion ranging from the Ohio River in central Kentucky to the inner Coastal Plain of Alabama and, east/west, from the Fall Zone of South Carolina and Georgia to eastern Mississippi and westcentral Tennessee. A disjunct population inhabits the Tunica Hills, along the eastern side of the Mississippi River in southwestern Mississippi and adjacent Louisiana. It is abundant in the Cumberland Plateau of Kentucky, Tennessee, and Alabama, but occurs only in the western tip of Virginia. The distribution skirts the western and southern peripheries of the Blue Ridge Province, including only certain border counties of North Carolina, primarily those adjoining Georgia and western South Carolina. The northward extension west of the Appalachians is much greater than that to the east, and sporadic records from the interior of North Carolina and southern border counties east of the Appalachians apparently constitute accidental human importations. Specific localities are detailed and plotted on a distribution map.

The southern unstriped scorpion, *Vaejovis carolinianus* (Beauvois) (Fig. 1), characterized by dusky brown pigmentation without stripes and the absence of a subaculear tubercle on the telson, is the only indigenous scorpion in the southeastern United States known to occur north of Florida (Muma 1967, Shelley 1994). Rossman (1979) presented a distribution map and summarized earlier records; Gibbons et al. (1990) mapped the overall distribution and that in Alabama, and reported that the scorpion occurs in scattered localities from central Kentucky, eastern Tennessee, and western parts of Virginia and the Carolinas through Georgia and Alabama, chiefly above the Coastal Plain. Gibbons et al. mentioned that isolated records were available for eastern and southwestern Mississippi, and the adjacent part of Louisiana, and that the scorpion ranges south of the Fall Zone in Alabama as far as Dallas County. However, the only specific locality reported in the latter areas is Tunica Hills, along the eastern side of the Mississippi River in West Feliciana Parish, Louisiana, and Wilkinson County, Mississippi, and

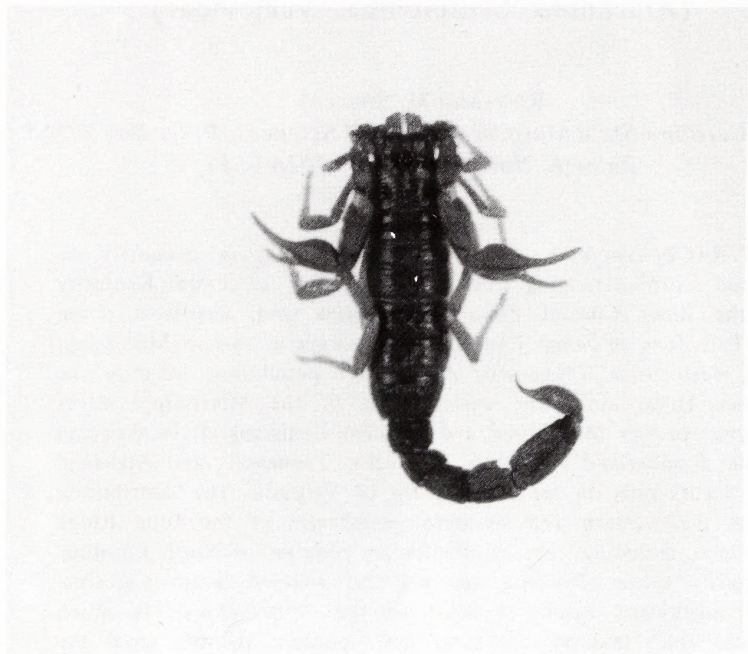


Fig. 1. *Vaejovis carolinianus*, dorsal view.

few definite sites of occurrence have ever been recorded. The only other published records known to me are the following by Brimley (1938) and/or Shelley (1975a):

KENTUCKY: *Laurel Co.*, 1 mi (1.6 km) W Baldrock. *Bell Co.*, Pineville.

VIRGINIA: *Lee Co.*, Cumberland Gap.

TENNESSEE: *Sevier Co.*, Pigeon Forge and Laurel Creek, Great Smoky Mountains National Park.

NORTH CAROLINA: *Cherokee Co.*, near Culberson and Murphy. *Polk Co.*, Tryon and Columbus.

SOUTH CAROLINA: *Pickens Co.*, Clemson. *Laurens Co.*, Laurens. *Lexington Co.*, Lexington.

GEORGIA: *Habersham Co.*, Tallulah Falls (incorrectly placed in Rabun County). *Fulton Co.*, Atlanta. *Clarke Co.*, Athens.

For the past 15 years, I have examined unreported museum samples of *V. carolinianus* and collected the scorpion in southeastern states; from these records a clear picture of the species' range has emerged

(Fig. 2). The purpose of this contribution is to document the distribution by providing specific localities and collection data, and to publish a dot map that eliminates ambiguities in previous maps, in which counties of occurrence are shaded. This procedure is misleading for peripheral areas like Lee County, Virginia, where *V. carolinianus* occurs only in Cumberland Gap, in the westernmost two miles of the County and State. Concerted efforts to find *V. carolinianus* eastward in Lee County have been unsuccessful (R. L. Hoffman, Virginia Museum of Natural History, personal communication), so shading the entire county incorrectly implies wider occurrence.

The overall distribution, as documented herein, extends southward through the Cumberland Mountains from the Ohio River, the northern boundary in central Kentucky, and spreads eastward to the Appalachians



Fig. 2. Distribution of *V. carolinianus*.

in southeastern Tennessee. The border then swings southward around the bulk of the Blue Ridge Province, penetrating border counties of southwestern North Carolina by spreading up river valleys from adjacent states. The easternmost natural occurrence in North Carolina is in Polk County; other records in this State are believed to represent accidental human importations (Shelley 1994). The distributional boundary then angles southeastward through the Piedmont Plateau of South Carolina to Columbia and follows the Fall Zone through Georgia into Alabama, before spreading onto the Gulf Coastal Plain in western Alabama and extending to the Mississippi River above Baton Rouge, Louisiana. Fewer specimens are available from the western side of its distribution, but *V. carolinianus* ranges northward through eastern Mississippi and western Tennessee to the Ohio River in central Kentucky; the only specimens taken farther west are those from Tunica Hills. Although these records still are somewhat scattered, they are continuous enough to suggest regular occurrence throughout the overall range except for the Tunica Hills population, which is disjunct. *Vaejovis carolinianus* is therefore an upland species occurring exclusively west of the Fall Zone in the Carolinas and Georgia. Where it extends onto the Coastal Plain in Alabama, it shows a marked preference for hills or ridges like Tunica Hills and the Lime and Buhrstone Hills, and the Chunnenugee Ridge, in Clarke County, Alabama. The scorpion has not been taken in the pine flatwoods that are abundant in the Coastal Plain of the Carolinas and Georgia. Muma (1967) considered *V. carolinianus* to be a potential inhabitant of the northern and panhandle counties of Florida, but the known distribution shows that this possibility is remote, even for the most proximate part of the State, i. e., the inner peripheries of Escambia and Santa Rosa counties in the western panhandle.

The greater northward extension west of the Blue Ridge Province, in contrast to that on the east, is particularly striking. East of the Appalachians, the range angles southeastward from Polk County, North Carolina, to Lexington County, South Carolina; to the west, however, it extends some 230 mi (368 km) farther north, to the Ohio River in central Kentucky. If the distribution east of the Appalachians were equivalent to that on the west, it would reach to around Charlottesville, Virginia! *Vaejovis carolinianus* is common in the Cumberland Mountains of Kentucky and Tennessee, as it also is in the western Blue Ridge Province in southeastern Tennessee. However, the only records from the western periphery of North Carolina are from Madison and Swain counties (Shelley 1994), which doubtlessly represent penetrations up the French Broad and Little Tennessee river valleys, respectively. The former also implies occurrence in adjacent Cocke County, Tennessee,

where the species has not been taken. The range swings northwestward from Sevier, and presumably Cocke, counties into the Cumberland Plateau and does not extend farther north in the Blue Ridge and Ridge and Valley Provinces.

Vaejovis carolinianus typically occurs in association with decaying pine logs, particularly beneath loose bark; it can be plentiful under loose rocks on talus slopes and has been encountered in mesic deciduous forests (Shelley 1975b, 1994). In central Tennessee, specimens have been taken at night with ultraviolet light from moss-covered vertical surfaces of old highway roadcuts in limestone, suggesting that the scorpions inhabit the cracks and crevices on these walls and forage either in the cracks or on the surface itself (W. D. Sissom, West Texas A&M University, personal communication). Rossman (1979) encountered specimens in clay soil on a stream bank, and beneath decaying logs, leaf litter, slabs of wood, and the bark of a dead hardwood tree. Gibbons et al. (1990) stated that *V. carolinianus* was restricted to moist woodland habitats, where it occurs beneath leaves, logs, and other litter. The scorpion occasionally wanders into buildings and has been collected in homes in Davidson County, Tennessee; Madison, Polk, and Transylvania counties, North Carolina; Laurens, Spartanburg, Lexington, and Oconee counties, South Carolina; and Tishomingo and Clarke counties, Mississippi. It was also taken in a dormitory room at Mississippi State University, Oktibbeha County, Mississippi.

The following locality records are supported by preserved specimens and are presented in alphabetical order; those from North Carolina are provided by Shelley (1994). Citations include the date of collection, the name(s) of the collector(s), and the repository, indicated by the following acronyms:

AMNH - American Museum of Natural History, New York,
New York.

ANSP - Academy of Natural Sciences, Philadelphia, Pennsylvania.

CAS - California Academy of Sciences, San Francisco.

CC - Biology Department, Columbus College, Columbus, Georgia.

CU - Entomology Department, Clemson University, Clemson
South Carolina.

FMNH - Field Museum of Natural History, Chicago, Illinois.

FSCA - Florida State Collection of Arthropods, Gainesville.

ILNHS - Illinois Natural History Survey, Champaign.

MCZ - Museum of Comparative Zoology, Harvard University,
Cambridge, Massachusetts.

MEM - Mississippi Entomological Museum, Mississippi State University,
Starkville.

- MMNS - Mississippi Museum of Natural Science, Jackson.
 MPM - Milwaukee Public Museum, Milwaukee, Wisconsin.
 NCDA - Pest Control Division, North Carolina Department of Agriculture, Raleigh.
 NCSM - North Carolina State Museum of Natural Sciences, Raleigh.
 NCSU - Entomology Department, North Carolina State University, Raleigh.
 NMNH - National Museum of Natural History, Smithsonian Institution, Washington, DC.
 NSC - Natural Science Center, Greensboro, North Carolina.
 RNH - Private collection of R. N. Henson, Boone, North Carolina.
 SEM - Snow Entomological Museum, University of Kansas, Lawrence.
 TAM - Entomology Department, Texas A&M University, College Station, Texas.
 UAAM - University of Arkansas Arthropod Museum, Fayetteville.
 UGA - University of Georgia Museum of Natural History, Athens.
 UL - Biology Department, University of Louisville, Louisville, Kentucky.
 UMMZ - University of Michigan Museum of Zoology, Ann Arbor.
 VMNH - Virginia Museum of Natural History, Martinsville.
 WDS - Private collection of W. D. Sissom, West Texas A&M University, Canyon, Texas.

KENTUCKY: *Bell Co.*, Pineville, 14 August 1952, collector unknown (CAS); Pine Mountain St. Pk., 7 August 1949, H. S. Dybas (FMNH), 2 May 1975, C. C. Cornett (UL), and June 1975 and 1976, J. K. Ettman (NCSM); Fern Lake nr. Middlesboro, 12 August 1959, T. Wolfe, W. L. Burget (AMNH, VMNH); Cumberland Gap, date unknown, W. Faxon (MCZ); and Balkan, 1927, C. F. Clayton (NMNH). *Bullitt Co.*, Fort Knox, date unknown, P. Burchfield (AMNH). *Bullitt/Nelson Cos.*, State Forest, 17 July 1947, H. Nadler (NMNH). *Jefferson Co.*, Ft. Knox, 7 September 1993, G. Kettring (UL). *Laurel Co.*, 1 mi (1.6 km) NW Baldrock, 26 May 1952, L. Hubricht (NMNH). *Lincoln Co.*, locality unknown, 22 May 1966, B. Carter (UL). *McCreary Co.*, Yahoo Falls and Cumberland Falls, 24 May 1972, collector unknown (UL). *Meade Co.*, Quarry off KY hwy. 1638, 12 July 1967, C. Karnella (UL). *Pulaski Co.*, Mt. Victory, 27 May 1972, collector unknown (UL). *Rockcastle Co.*, 3 mi (4.8 km) N Mt. Vernon, Renfro Valley, 10 June 1954, R. Barbour (NCSM). *Taylor Co.*, Campbellsville, 7 May 1956, collector unknown (FSCA). *Wayne Co.*, locality and collector unknown, 21 September 1994 (UL). *Whitley Co.*, Cumberland Falls St. Pk., nr. Cumberland Falls, 27 June 1945 collector unknown (CAS); and 0.5 mi (0.8 km) E Cumberland Falls St. Pk., 10 October 1992, R. W. VanDevender (RNH).

VIRGINIA: *Lee Co.*, 0.5 mi (0.8 km) N Cumberland Gap, Willis Hollow, 15 July 1958, C. Stoddard, W. L. Burget (AMNH, VMNH); and Cumberland Gap, above Cudjo's Cave, 23 June 1950, J. H. Fowler (CAS).

TENNESSEE: *Anderson Co.*, Oak Ridge, August 1962, H. Phillips (NMNH). *Blount Co.*, Great Smoky Mts. Nat. Pk., The Sinks, 19 June 1960, I. McClurkin (FSCA); Chilowhee Mts., 21 July 1965, C. L. Wilder (VMNH); and Townsend, 19 June 1960, I. McClurkin (FSCA). *Cheatham Co.*, Ashland City, summer 1994, R. Stevens (NCSM). *Claiborne Co.*, Cumberland Gap, 11 June 1933, H. W. Chickering (MCZ). *Cumberland Co.*, 11 mi (17.6 km) NNW Crossville, US hwy. 127 at Lickfork Cr., 9 June 1979, R. M. Shelley, R. K. Tardell (NCSM). *Davidson Co.*, Goodlettsville, 19 December 1949, Ross, Stannard (ILNHS); ca. 1.5 mi (2.4 km) SW Marrowbone L., 28 April 1991, D. McGinnity (WDS); and Nashville, 23 May 1985, K. Collier (WDS). *DeKalb Co.*, Edgar Evins, St. Pk., 20 May 1983, R. W. VanDevender (RNH); and 6 mi (9.6 km) NE Smithville off TN hwy. 56 on S side Center Hill L., 20 July 1984, W. D. Sissom, C. N. McReynolds (WDS). *Hamilton Co.*, Chattanooga, October 1932, L. Trenholm (NMNH). *Hardin Co.*, Savannah, 1960, collector unknown (AMNH); Counce, YMCA camp nr. Pickwick Dam, 5 August 1966, A. Smoot (AMNH); and Pickwick Dam, 29 September 1963, M. Lou (CAS). *Madison Co.*, Jackson, 1958, A. F. Archer (AMNH). *Marion Co.*, US hwy. 64, 2.9 mi (4.6 km) E jct. TN hwy. 156, 26 March 1979, R. Franz, R. E. Ashton, A. L. Braswell (NCSM); 6 mi (9.6 km) S Jasper, along TN hwy. 156A, 0.2 mi (0.3 km) N AL line, 21 May 1983, R. M. Shelley, J. Staton (NCSM). *Morgan Co.*, locality unknown, 28 August 1976, J. C. Mitchell, J. Byrd, J. Kline (VMNH); and Catoosa WRA, between Lookout & Phil, 8 May 1976, R. L. Jones (MCZ). *Pickett Co.*, Pickett St. Pk., 1 May 1935, H. Augusby (NMNH). *Polk Co.*, exact site unknown, April 1985, R. W. VanDevender (RNH); and Parksville Reserve, 7 August 1936, M. H. Hatch (AMNH). *Putnam Co.*, 2 mi (3.2 km) E Cookeville, along I-40, date and collector unknown (FMNH). *Rhea Co.*, 3 mi (4.8 km) N Spring City, 26 June 1962, F. N. Young (FSCA); and Spring City, August 1919, E. R. Dunn (MCZ). *Roane Co.*, nr. Harriman, 11 July 1933, W. Ivie (AMNH); and Kingston, 12 and 14 July 1933, W. J. Gertsch, W. Ivie (AMNH) and 15 April 1952, G. E. Smith (AMNH). *Rutherford Co.*, ca. 7.4 mi (11.8 km) E Murfreesboro, along US hwy. 70S at Cripple Cr., 18 April 1973, Czajka, Ketchum (MPM). *Sevier Co.*, Pigeon Forge, 29 August 1943, J. A. Bell (CAS). *Van Buren Co.*, Fall Creek Falls St. Pk., 11 August 1951, T. Cohn (AMNH). *Warren Co.*, nr. McMinnville, along TN hwy. 8, 15 August 1971, M. A. Morris (ILNHS). *White Co.*, Rock Island, 18 April

1917, collector unknown (NMNH). *Wilson Co.*, Cedars of Lebanon St. Pk., 16 April 1976, R. L. Jones, A. C. Ecternauer (MCZ).

NORTH CAROLINA: *Cherokee, Columbus, Guilford, Haywood, Iredell, Madison, Mecklenburg, Polk, Swain, Transylvania, Wake, and Yancey* counties, as per the listing in Shelley (1994) (NCSM, NCSU, NMNH, NSC, RNH, SEM).

SOUTH CAROLINA: *Abbeville Co.*, Sumter Natl. For., FS rd. 505 at Long Cane Scenic Area, 14 September 1980, R. M. Shelley, M. Morgan (NCSM). *Anderson Co.*, Pendleton, Aldwood, 18 May 1985, J. H. Morse (CU); and along US hwy. 29, exact site unknown, July 1989, A. Hill (RNH). *Edgefield Co.*, 11.4 mi (18.2 km) W Edgefield, SC hwy. 68, 0.2 mi (0.3 km) N jct. US hwy. 52, 8 August 1976, R. M. Shelley (NCSM). *Greenville Co.*, nr. NC border, exact location unknown, 29 August 1929, collector unknown (NMNH); and Greenville, date and collector unknown (ANSP) and Camp Sevier, WWI Army Post probably now in Greenville, date unknown, J. Leidy (ANSP). *Laurens Co.*, Kinards, 15 May 1975, G. F. Smith (NCSU); and Laurens, 1 November 1955, collector unknown (CAS). *Lexington Co.*, nr. Chapin on L. Murray, 19 February 1991, F. Authinreith (RNH); Leesville vic., 26 September - 7 October 1949, L. Brodie (FMNH); and Lexington, date and collector unknown (CAS). *McCormick Co.*, locality unknown, 1935, collector unknown (NMNH) and 15 June 1958, collector unknown (MCZ); and De La Howe Forest, 10 July 1942, C. J. Goodnight (ILNHS). *Newberry Co.*, Newberry, July 1932, L. A. Savage (NMNH). *Oconee Co.*, Mountain Rest, 1973, R. F. Shriner (NMNH); Oconee St. Pk., 10 June 1991, E. G. Riley (TAM); South Cove Landing, date unknown, A. Dozier (FSCA); nr. Clemson, 22 September 1985, J. R. Mayer (NCSU); and 6.8 mi (10.9 km) S Westminster, along SC hwy. 67 at Choestoea Cr., Hartwell Res., 10 June 1978, R. M. Shelley, W. B. Jones (NCSM). *Pickens Co.*, 7 mi (11.2 km) NE Pickens, 16 October 1976, collector unknown (FSCA); and Clemson, 3 December 1926 and April 1928, C. S. Brimley (NCDA), 25 September 1928, R. C. Fox (CU), February 1930, F. Smith (UAAM), 16 March 1940, E. C. Van Dyke (CAS), 22 April 1968, H. Harris (CU), and 8 September 1976, S. Prichard (CU). *Saluda Co.*, Saluda, 15 June 1958, N. B. Causey (MCZ); and 8 mi (12.8 km) SW Leesville, along Brodie Rd., September 1992, B. Cockerel (RNH). *Spartanburg Co.*, Landrum, 4 August 1910, R. V. Chamberlin (AMNH); and Glenn Springs, 17 October 1984, H. B. Matthews (NCSU).

GEORGIA: *Baldwin Co.*, Milledgeville, 2 August 1894, collector unknown (NMNH). *Bartow Co.*, E of Cartersville, along GA hwy. 21, 1.8 mi (2.9 km) E jct. hwy. I-75, 17 March 1984, G. T. Baker (MEM). *Butts Co.*, Indian Springs, date unknown, L. M. Underwood (NMNH).

Clarke Co., Athens, 1 October 1936, H. O. Lund (AMNH), 11 October 1960-30 October 1972, N. Bein, W. Eissler, R. Muha, K. Douce (UGA), and 27 November 1983, M. LaSalle (MEM); and Whitehall For., 9 July 1977-21 May 1984, C. L. Smith (UGA). *Cobb Co.*, Austell, date unknown, N. Banks (MCZ); and Kennesaw Mtn., 26 April 1963, P. W. Fattig (NMNH). *Columbia Co.*, Harlem, 25 July 1962, G. Jordan (FSCA). *DeKalb Co.*, Atlanta, September 1982, collector unknown (RNH); Stone Mtn., 15 June 1958, N. B. Causey (MCZ) and 25 August 1966, Trobinck (FSCA); and Dunwoody, Summerbrook Dr., September 1991, A. L. Henson (RNH). *Elbert Co.*, Bobby Brown St. Pk., 31 July 1977, R. M. Shelley (NCSM); and 11 mi (17.6 km) ENE Elberton, along GA hwy. 368 at Pickens Cr., 20 July 1979, R. M. Shelley, R. K. Tardell (NCSM). *Floyd Co.*, Rome, Marshall For., 17 March and 25 April 1963, J. Parker (NMNH). *Fulton Co.*, Roswell, date unknown, Mrs. King (MCZ); Atlanta, 27 June 1943, H. Hoogstraal (FMNH), March 1945 and 21 September 1951, collector unknown (CAS), August 1951, G. W. Fraser (NMNH), and 1957, H. D. Pratt (ILNHS); Chamblee, 15 September 1952, collector unknown (ILNHS). *Gordon Co.*, Horn Mtn., 12 June 1986, J. D. Lazell (NMNH). *Habersham Co.*, Tallulah, 1-4 July 1955, R. B. & R. L. Hoffman (NMNH); Tallulah Falls, 1 April 1891 and April 1897, L. M. Underwood (NMNH); N of Clarkesville, 27 April 1943, W. Ivie (AMNH); and between Clarkesville and Toccoa, 28 April 1943, W. Ivie (AMNH). *Harris Co.*, exact sites unknown, June 1982-August 1992, J. A. Layne, P. Jones, H. M. Johnson, B. A. Craighton, J. A. Riley, J. Chappell, and R. D. Schiavone (CC). *Jackson Co.*, locality not specified, 29 September 1960, Moody (UGA). *Lumpkin Co.*, Frogtown Gap, 31 May 1934, F. Harper (AMNH). *McDuffie Co.*, between Thomson and Washington, 22 April 1943, W. Ivie (AMNH). *Meriwether Co.*, Warm Springs, 4 May 1935, collector unknown (NMNH). *Monroe Co.*, Forsyth, 1962, A. F. Archer (AMNH). *Murray Co.*, Fort Mtn. St. Pk., 14 July 1952, P. M. Choate (FSCA). *Muscogee Co.*, Columbus, 25 April 1971, W. M. Petrsek (CC) and 5 April 1982, J. Losonsky (CC). *Newton Co.*, Covington, 17 November 1984, J. Wheeler (NMNH). *Putnam Co.*, 8 mi (12.8 km) S Eatonton, Oconee Nat. For., 22 May 1981, J. M. Carpenter (MCZ). *Rabun Co.*, Rabun Jct., April and August 1887, collector unknown (NMNH); and Clayton, 6-12 April 1940, E. C. Van Dyke (CAS) and 5-9 September 1959, K. Ulman (AMNH). *Rockdale Co.*, along Big Haynes Cr., 16 September 1976, T. Schowalter (UGA). *Stephens Co.*, Toccoa Lake, 10 October 1928, collector unknown (NMNH); and Toccoa, June 1953, R. L. Hoffman (NMNH). *Taliaferro Co.*, Crawfordville, 30 July 1971, M. & M. Cazier (WDS). *White Co.*, Unicoi St. Pk., 8 July 1973 and 25 May 1975, H. O. Lund (UGA); and Sautee, 13 September 1959,

H. O. Lund (UGA). *County Unknown*, Gowerville, date unknown, S. M. King (MCZ).

ALABAMA: *Bibb Co.*, nr. Wilton, 28 July 1962, R. E. Crabill, A. B. Gurney (NMNH). *Chambers Co.*, Fairfax, 1949-1950, A. F. Archer (AMNH). *Chilton Co.*, Maplesville, date and collector unknown (FSCA); and Verbena, 22 July 1900, W. R. Maxon (NMNH). *Clarke Co.*, Thomasville, 6 August 1933, C. E. Burt (NMNH); and Camp Maubila, a Boy Scout camp. ca. 6 mi (9.6 km) S Grove Hill, 4 mi (6.4 km) E US hwy. 43, 23 June 1983, P. Cross (MEM). *Clay Co.*, Cheaha Mtn., 3 September 1969, J. G. E. Rehn (ANSP). *Cleburne Co.*, locality unknown, 8-9 September 1946, collector unknown (FSCA); and Talladega Natl. For., 28 July 1962, R. C. & A. Graves (FSCA). *Coosa Co.*, Hatchet Cr., 4 June 1940, A. F. Archer (AMNH). *Cullman Co.*, Cullman, St. Boniface Col., 17 June 1958, collector unknown (FSCA). *DeKalb Co.*, Desoto St. Pk., 10 May 1986, R. F. C. Naczi (UMMZ) and 18-19 May 1990, D. Hildebrandt, T. L. Schiefer (MEM); and Collinsville, 10 July 1962, H. B. Cunningham (ILNHS). *Franklin Co.*, Ezell Cave, along AL hwy. 1060, 8 November 1969, F. Shires (NCSM). *Jackson Co.*, 12 mi (19.2 km) N Scottsboro, National Bridge Cave, August 1970, R. C. Graham (NCSM). *Lauderdale Co.*, Wilson Dam, 13 July 1942, J. W. Belkin (AMNH) and June 1953, R. V. Schick (AMNH). *Lee Co.*, Auburn, November 1895 and July 1896, L. M. Underwood (NMNH). *Madison Co.*, Huntsville, Monte Sano St. Pk., date unknown, Rosenberg (FSCA); E of Huntsville, SW slope of Round Top Mtn., 19 July 1988, K. Woodstock (NMNH); and Monte Sano St. Pk., 1946, J. Murphy (AMNH). *Morgan Co.*, locality and collector unknown, 27 July 1910 (AMNH). *Russell Co.*, exact site unknown, 29 July 1990, T. Mann (CC). *Tallapoosa Co.*, Dadeville, 13 July 1914 (NMNH); and Alexander City, 31 October 1944, G. Nelson (MCZ). *Tuscaloosa Co.*, Lake Lurleen St. Pk., 18 May 1988, C. M. & O. S. Flint (NMNH). *Walker Co.*, Forks of Warrior R., 20 October 1912, H. Smith (AMNH). *Winston Co.*, Double Springs, 18 June 1958, N. B. Causey (MCZ).

MISSISSIPPI: *Clarke Co.*, 0.8 mi (1.3 km) N Hurricane Cr., 3 December 1961, L. Hubricht (NMNH); and at AL line, 5.0 mi (8.0 km) SE Lauderdale Co. line, 17 April 1987, R. L. Jones, J. Wiseman (MMNS). *Oktibbeha Co.*, Starkville, Mississippi St. Univ., 3 October 1983, collector unknown (MEM). *Tishomingo Co.*, Iuka, 31 October 1988, B. Hopper (MEM); and Tishomingo St. Pk., 28 July 1983, P. R. Miller (MEM).

No specimens were available from the following additional, generalized county records of Benton (1973), Rossman (1979), and Gibbons et al. (1990). Dots are therefore placed centrally in these counties in Figure 2:

KENTUCKY: *Jackson, Larue, Lee, and Leslie* counties.

TENNESSEE: *Claiborne, Grundy, and Monroe* counties.

GEORGIA: *Cherokee, Crawford, Dade, and Polk* counties.

ALABAMA: *Calhoun, Colbert, Dallas, Elmore, Fayette, Hale, Lawrence, Marion, Randolph, and Shelby* counties.

MISSISSIPPI: *Lauderdale* County.

The following additional localities were communicated by H. L. Stahnke (*in litt.*) based on specimens in his personal collection, now housed at the CAS. These samples were not represented in the material loaned from that institution, but they are considered accurate and are hence incorporated into Figure 2.

KENTUCKY: *Meade Co.*, Muldraugh.

TENNESSEE: *Blount Co.*, Great Smoky Mountains Nat. Pk., 1 mi (1.6 km) S The Sinks, and along Little Tennessee R. at Long Arm Bridge. *Sevier Co.*, Gatlinburg.

ALABAMA: *Jefferson Co.*, Adger. *Tuscaloosa Co.*, Peterson.

MISSISSIPPI: *County Unknown*, Pine Flat.

The following localities, communicated verbally by J. L. Knight (South Carolina State Museum, Columbia), are also incorporated into Figure 2.

SOUTH CAROLINA: *Aiken Co.*, North Augusta, S of I-20 along N side of Savannah River. *Lexington Co.*, West Columbia. *McCormick Co.*, L. Thurmond.

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NSC, and J. Knight did likewise for specimens at the SCSM. D. S. Lee also reviewed a preliminary draft of the manuscript. Figure 1 is courtesy of D. J. Lyons, NCSM exhibits designer.

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Atlantic Ocean Occurrences of the Sea Lamprey,
Petromyzon marinus (Petromyzontiformes:
Petromyzontidae), Parasitizing Sandbar, *Carcharhinus*
plumbeus, and Dusky, *C. obscurus* (Carcharhiniformes:
Carcharhinidae), Sharks off North and South Carolina

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ABSTRACT—Sandbar and dusky sharks captured in 1993 in western Atlantic Ocean waters off North and South Carolina were parasitized by sea lampreys. All lampreys were females ranging from 165 to 343 mm total length. Removal of an attached lamprey revealed round, reddish and/or bleeding areas on a shark's body. Blood oozing from a lamprey's cloaca indicated that feeding was occurring or had occurred.

The anadromous parasitic sea lamprey (*Petromyzon marinus*) is widely distributed on both sides of the Atlantic Ocean. It occurs off North America from Labrador southward to Florida, and along eastern Europe from Varanger Fjord in Norway to the western Mediterranean (Beamish 1980). Apparently it also formerly occurred in the Gulf of Mexico (Vladykov and Kott 1980, Gilbert and Snelson 1992). Lampreys are known from marine waters to depths of 4,099 m (Haedrich 1977). Dempson and Porter (1993) note other western Atlantic captures of sea lampreys in deep open ocean waters. Excellent reviews of sea lamprey biology can be found in Hardesty and Potter (1971) and in the Proceedings of the Sea Lamprey International Symposium (1980). We add the sea lamprey as an external parasite of sharks and present meristic and morphometric data for specimens captured off North and South Carolina.

Sea lampreys prey on a variety of fishes in freshwater and marine habitats (Bigelow and Schroeder 1948). Sea lampreys have not been reported from ocean habitats off North Carolina (personal observation) or South Carolina (S. Van Sant, South Carolina Marine Resources Center, personal communication), although lamprey captures are known from inland North Carolina streams and Albemarle Sound (Smith 1907, Menhinick 1991). Schwartz et al. (1982) reported a 140-mm total length (TL), 3.9-g specimen (UNC 8501) entangled in a gill net on the west side (Station 19 west) of the Cape Fear River, 4 km north of Southport, North Carolina, from waters of 10.2C and 10 ppt salinity on 19 February 1974. Whether it was attached to a fish caught in the net was unknown.

PREVIOUS SEA LAMPREY—SHARK PARASITISM RECORDS

We know of two verified records of sea lamprey—shark parasitism. One involves a female sea lamprey and a basking shark (*Cetorhinus maximus*), specimen 965-2-3-1, of the Nova Scotia Museum (Bigelow and Schroeder 1948). The lamprey was 290-mm TL when preserved in formalin. The 7.6-m-long basking shark, caught 29 June 1965 in a gill net off Hopson Island (near Prospect), Halifax County, Canada, was alive when the lamprey was removed. Attachment was just above and anterior to the base of the anal fin, although sea lampreys often attach to pectoral fins and along the dorsal and body sides (Cochran 1985, 1986). The second was a record of two adult lampreys, 180- and 250-mm TL (USNM 130791) taken from an unknown species of shark captured 3 June 1885 off Cape Charles, Virginia, at Albatross Station 2422 at 37°08'30"N, 74°33'30"W (Jenkins and Burkhead 1993).

RECENT SEA LAMPREY—SHARK PARASITISM RECORDS

South Carolina—We captured a female sea lamprey (UNC 17398), 168-mm TL, 8.8 g, on 6 February 1993 while longlining 69 km off South Carolina in 31.1 m of water. Set location began at 33°10.9'N, 78°17.45'W and ended at 33°00'N, 78°24.08'W. It was still attached to a 1280-mm fork length (FL), male sandbar shark (*Carcharhinus plumbeus*) along the shark's right lateral flank midway between the rear tips of the pelvic and dorsal fins on the gray portion of the skin. Removal of the lamprey revealed a round reddish area on the side of the body, which indicates that it had been attached for some time before the shark's capture. Blood oozed freely from the female lamprey's cloacal opening.

North Carolina—We know of five recent occurrences (March 1993) of female sea lampreys parasitizing sharks captured from two different locations off North Carolina; the host in one case was a 3-m-FL dusky shark (*Carcharhinus obscurus*), the others three 3-m-FL sandbar sharks (*C. plumbeus*). A dusky shark and one sandbar shark, captured by fishermen longlining 74-km east-southeast off Masonboro, North Carolina, carried one feeding lamprey attached near the cloaca of each shark. But the lampreys were not retained by the fishermen who captured the sharks.

Three additional female sea lampreys (UNC 17403, Table 1) 165-, 178-, and 343-mm TL, weighing 6.4, 9.5, and 70.7 g, respectively, were captured 23 March 1993 during nighttime longlining sets 46.2 km east of Cape Lookout in 31–36-m waters. All three specimens parasitized 3-m-TL female dusky sharks, one was attached to a pelvic fin, the others to the white skin of the cloacal area. No masses were taken of any shark at sea. Body proportions of the North Carolina preserved sea

Table 1. Meristic and morphometric data for sea lampreys captured parasitizing dusky and sandbar sharks caught off South Carolina (UNC 17398) and North Carolina (17403), 1993. Lengths are expressed as a percentage of the total length.

Lengths (% total length)	Female Sea Lampreys			
	UNC 17398 ¹	UNC 17403 ²		
Predorsal	14.9	15.3	15.2	13.1
Branchial	10.8	8.7	8.8	8.7
Disc	9.0	9.3	9.3	8.5
Eye	3.3	3.0	2.2	2.3
Trunk	45.1	46.1	49.7	53.6
Tail	29.1	29.8	26.2	24.5
Myomere	68	66	67	— ³
Total Length (mm)	168	165	178	343

¹Host female sandbar shark.

²Hosts all female dusky sharks.

³Dark adult body coloration prevented accurate myomere count.

lampreys (Table 1) were larger than those reported for a 136-mm-TL specimen from Florida (Vladykov and Kott 1980).

CONCLUSIONS

Sea lamprey-shark parasitism occurrences are rarely reported because fishermen or scientists often think that a reddened bleeding area on the body is simply a bruise rather than a wound caused by a lamprey. Likewise, a lamprey might have fallen off once a shark was landed, making the association of the injury with a lamprey difficult. Information on sea lampreys from sharks caught at sea may shed more information on their occurrence, seasonality, water depth frequented, host preferences, and biology of sea lampreys than is presently known. Lamprey parasitism may be more damaging to marine fishes than now suspected.

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Roanoke College, Salem, Virginia, was helpful with the early Virginia lamprey record. L. White typed the text.

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Clutch Parameters of *Storeria dekayi* Holbrook (Serpentes: Colubridae) from Southcentral Florida

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ABSTRACT—I examined clutch characteristics from a series of *Storeria dekayi* collected in southcentral Florida from March to July 1990. Clutch size averaged 8.5 and was not significantly associated with female body size. The small clutch sizes of this sample conformed to predictions of clutch size reduction in southern populations. However, the data did not support predictions of increased clutch number in southern populations. Possibly, high relative clutch mass detected in this population and an unaltered breeding season hinder production of more than one clutch annually.

Two latitudinal clines in snakes have been proposed that predict differences in clutch size and number along a geographic gradient. The first predicts a decrease in clutch size from north to south (Fitch 1985). The second hypothesis predicts an increase in clutch number at lower latitudes concomitant with a longer reproductive season (Fitch 1970).

The reproductive biology of *Storeria dekayi* in Florida is poorly known; however, parturition dates of this species are available from Florida (Iverson 1978), and they do not differ from parturition dates in more northern populations (Fitch 1970). Iverson's (1978) data do not support the prediction of a latitudinal cline in clutch number for this species.

With few exceptions, Iverson (1978) found that most Florida snake species he examined did not conform to the prediction of multiple clutches in southern populations. In this article I present additional reproductive data for female *S. dekayi* from south Florida which permit testing Fitch's (1985) hypothesis of clutch size reduction in southern populations and further evaluation of the likelihood of multiple clutch production in this species at the southern limit of its geographic range (Fitch 1970).

METHODS

Snakes were collected from 1830 to 2200 hours from a paved road (C-621) near Lake Placid, Highlands County, Florida, during March-July 1990. All snakes observed were collected, frozen within 3 hours of capture, and dissected the next day.

Condition of follicles was staged according to Kofron (1979). I estimated clutch size by counting enlarged follicles or conceptuses. Relative clutch mass, the quotient of clutch mass divided by the sum of the clutch mass and the female body mass (Seigel and Fitch 1984), was measured in females with fully developed conceptuses. All specimens are located in the Archbold Biological Station vertebrate collection.

RESULTS AND DISCUSSION

Eighteen snakes (3 males, 15 females) were collected during 22.5 hours of searching. Snout-vent lengths (SVL) of males collected in March ($n = 1$) and June ($n = 2$) were 23.0, 25.0, and 27.5 mm, respectively. Snout-vent lengths and clutch parameters of females are summarized in Table 1. Estimated clutch size was not significantly correlated with SVL ($r = 0.31$, $P > 0.05$).

Table 1. Snout-vent lengths (SVL) and clutch parameters of *Storeria dekayi* collected from one location in Highlands County, Florida, 1990.

Date	Female SVL	Clutch Size	Relative Clutch Mass	Neonate SVL (cm)
17 March	24.6	7		
17 March	21.8	7		
17 May	26.0	12	0.400	6.3 + 0.306
25 May	28.0	spent		
29 May	24.3	8	0.361	
31 May ¹	25.3	9		7.7 + 0.500
8 June	26.0	spent		
8 June	29.0	11		
14 June	28.0	10	0.340	8.4 + 0.097
21 June	27.5	5		
21 June	27.5	10		
24 June	26.5	8		
3 July	33.0	9		
23 July	26.0	5		
24 July	28.5	10		
31 July	25.3	9		
\bar{x}	26.8	8.5	0.367	
SD	2.55	2.15	0.030	
Range	21.8–33.0	5–12	0.340–0.400	
n	15	13	3	

¹ Denotes a specimen collected in 1992 from the same site. Data not analyzed with 1990 sample.

Mean clutch size (8.5) was similar to that found in Everglades National Park by Dalrymple et al. (1992), and the samples from both regions had a female - biased sex ratio. Female *S. dekayi* from Iverson's (1978) northern Florida sample had smaller SVL than females from my study ($t = 3.681$; $df = 10$; $P < 0.004$), but the two samples did not differ significantly in clutch size. Although both mean female SVL (27.3 mm) and clutch size (14.0) from *S. dekayi* near Lake Erie (King 1993) were significantly larger than those of my study ($t = 2.12$ $P = 0.05$; and $t = 7.53$ $P < 0.00$, respectively; $df = 38$), the difference in SVL was marginal. Mean clutch sizes, 14.9 in Louisiana (Kofron 1979) and 14 in New York (Clausen 1936), are also substantially larger than those for Florida, which supports Fitch's (1985) prediction of smaller clutch sizes in southern latitudes.

A review of relative clutch mass in snakes indicates that there is a reduction in relative clutch mass among viviparous forms that may reduce the risk of mortality in gravid females (Seigel and Fitch 1984). The cost of lowering relative clutch mass is a reduction of clutch size, offspring size, or both. Resources could limit production of more than one clutch (Bull and Shine 1979), but a large clutch could compensate for a single brood (Seigel and Fitch 1984). Mean relative clutch mass in *S. dekayi* from southern Florida was high (0.367) and similar to that (0.372) recorded for *S. dekayi* from Maryland (Jones 1976). A high relative clutch mass in southern Florida *S. dekayi* may compensate for a single small clutch produced each season.

In northern Florida, females with fully developed conceptuses were recorded from July to September (Iverson 1978). In southern Florida, the earliest date was May (Iverson 1978, my study), and in Everglades National Park captive females gave birth from June to September (Dalrymple et al. 1992). Collectively, the breeding season of Florida populations of *S. dekayi* (Iverson 1978, Dalrymple et al. 1992, my study) falls within the range of other populations (Fitch 1970, Kofron 1979). Further, my results did not indicate a reduction of relative clutch mass, which could facilitate multiple clutch production, in southern Florida *S. dekayi*.

CONCLUSIONS

Clutch frequency of this species in southern Florida has not been determined to date, and multiple clutch production, even if infrequent, has not been excluded. An annual sample of specimens or mark-recapture will best answer this question. Results of my study do not support Fitch's (1970) prediction of multiple clutch production by *S. dekayi* in the southern part of the range.

However, clutch sizes from south Florida *S. dekayi* were smaller than northern populations as predicted by Fitch (1985) and unaffected by female body size. Possibly, a high relative clutch mass and an unaltered breeding season limit this population to one brood annually.

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Influence of Environmental Conditions on Flight Activity of *Plecotus townsendii virginianus* (Chiroptera: Vespertilionidae)

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ABSTRACT—Flight activity of the Virginia big-eared bat (*Plecotus townsendii virginianus*) was measured in relation to eight environmental variables during 1990 and 1991 in Lee County, Kentucky. Activity, measured as the mean nightly detection frequency of bats fitted with transmitters, was positively related to percent relative humidity and negatively related to moon phase and wind speed. Multiple regression analysis showed relative humidity to have the strongest association with flight activity of all the environmental variables tested. An explanation for this pattern was that bats reduced their foraging activity on nights of low relative humidity to avoid excess water loss because of extremes in vapor pressure deficits during flight. Other explanations for the observed activity patterns may exist, but they were not investigated in our study.

A wide range of abiotic environmental variables affect flight activity of bats, including sunlight, moonlight, temperature, wind speed, and precipitation. Sunlight inhibits flight activity and serves to synchronize circadian periodicity (Erkert et al. 1980). Moonlight reduces flight activity (Erkert 1974) and is known to induce shifts in foraging patterns (Fenton et al. 1977). Flight activity of bats increases with temperature, with shorter activity periods on cooler nights (Anthony et al. 1981) and extended bouts of activity on warmer nights (O'Farrell et al. 1967). Sufficiently strong winds suppress flight activity (O'Farrell et al. 1967), but the influence of slower air speeds, if any, is unknown.

Responses of bats to precipitation is not consistent among, or even within, species. Heavy rainfall reduced flight activity of *Pipistrellus pipistrellus* (Stebbins 1968), but did not do so in another study (Swift 1980). The timing of rainfall events is important (Felton et al. 1977), with rain at dusk known to delay nightly emergence in *Nycticeius humeralis* (Watkins 1972).

In contrast, effects of relative humidity on flight activity of bats have been suggested (Watkins 1972, Lacki 1984) but quantitative data are lacking. Studies have demonstrated the importance of water balance to bats under both laboratory (Bassett 1980, Bassett and

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Wiebers 1980) and free-ranging conditions (Kurta et al. 1989, Kurta et al. 1990). This would suggest that selection for adaptations to minimize water loss should evolve in bats, particularly in association with flight because of the high surface area to volume ratio of bat wings.

Bats inhabiting arid environments show a direct relationship between urine concentrating ability and evapotranspiration to precipitation ratio (Bassett 1986). In wetter regions, bats should encounter fewer problems of water balance. Flexibility in foraging strategy, such as reduced activity on less humid nights (i.e., increased vapor pressure deficits), should help to maintain water balance.

Using radio telemetry we monitored flight activity of a temperate zone insectivorous bat, *Plecotus townsendii virginianus*, and related observed activity patterns with data for local environmental conditions. We tested the hypothesis that flight activity of *P. t. virginianus* is reduced as relative humidity declines, which would be expected if water balance is a critical selective pressure for temperate zone bats.

METHODS

The study area was located in the Cumberland Plateau, Lee County, Kentucky. Lee County is 80% forested and sparsely populated by humans (Newton et al. 1974). Mixed mesophytic forest is the dominant habitat (Braun 1950) with most stands being second growth timber because of past logging practices. The climate of the region is temperate, characterized by warm and humid summers and moderately cold winters. Average maximum and minimum temperatures are 34C in August and -18C in January (Newton et al. 1974). Average monthly precipitation is 9 cm (Newton et al. 1974). July and October are the wettest and driest months, respectively. Additional site details are provided by Adam et al. (1994).

Sixty bats were fitted with transmitters during 1990 and 1991, 30 each summer. Because this subspecies is very sensitive to disturbance (Bagley 1984), we studied males in 1990 and females in 1991 and addressed any problems that occurred with males in 1990 before handling females in 1991. Bats were mist-netted as they emerged from bachelor and maternity roosts, along cliffs, and on an abandoned logging road. Bats were weighed, sexed, aged, and then fixed with a 0.8-g transmitter (Type BD-2A, 172-173 MHz; Holohil Systems, Ltd., Ontario, Canada, and Wildlife Materials, Inc., Carbondale, Illinois) on the dorsum between the scapulae. The surface was prepared by trimming the fur with scissors and applying surgical cement designed to hold the transmitter for about 10 days.

Three telemetry periods, each spanning five nights, were conducted in each year. In 1990 male bats were radiotracked from 2 to 6 June ($n = 9$ bats), 16 to 20 July ($n = 10$), and 6 to 10 August ($n = 11$). In 1991 females were tracked from 10 to 14 May ($n = 9$), 17 to 21 June ($n = 10$), and 5 to 9 August ($n = 11$). Bats were tracked from both fixed and mobile stations. Fixed stations were positioned on the top of cliffs enclosing a hollow with either a bachelor or maternity roost. Distances between fixed stations averaged 857 m in 1990 and 509 m in 1991. Mobile stations were along road routes throughout the surrounding areas. Three TRX1000s receivers (Wildlife Materials, Inc., Carbondale, Illinois) were used to locate bats, with an additional TRX2000s receiver used in 1991. Receivers were coupled to a 3- or 5-element yagi antenna. Signals were searched for at 20-minute intervals from sunset to sunrise. Bats may have been detected in multiple intervals by more than one receiver.

Telemetry data were organized into nightly rates of bat activity by converting signal responses into mean nightly detection frequencies (*NDF*) calculated as

$$NDF = \frac{t}{j=1} \left(\sum_{i=1}^n (d/o)/n \right) t^{-1}$$

where *NDF* = mean nightly detection frequency, t = number of time intervals post-sunset, n = number of bats with transmitters, d = number of receivers detecting a bat in an interval, and o = number of receivers operating in an interval.

Patterns of activity were also derived for each sampling period by converting signal responses to mean detection frequencies per time interval (*TIDF*) calculated as

$$TIDF = \frac{k}{j=1} \left(\sum_{i=1}^n (d/o)/n \right) k^{-1}$$

where *TIDF* = mean detection frequency per time interval, and k = number of days sampled.

Nightly environmental conditions were obtained from the Heidelberg, Kentucky, weather station located 11 km, from the bachelor roost. The foraging radius of bats from the bachelor and maternity colonies was large (Adam et al. 1994), rendering sampling for environmental conditions throughout the study site impractical. Data for eight variables were analyzed: daily maximum temperatures ($^{\circ}\text{C}$), daily minimum temperature ($^{\circ}\text{C}$), total precipitation the day of sampling (cm), total precipitation on the day preceding sampling (cm), average daily

relative humidity (%), average daily wind speed (km/hr), average daily barometric pressure (millibars), and moon phase (% of full moon illumination).

We initially tested *NDF* against all environmental variables separately using simple linear regression, and only those variables meeting the 0.10 probability level were retained. Backwards stepwise multiple regression was then used for modeling *NDF* against environmental variables. A probability of >0.10 was used for removal of a variable from the model. Data for 1990 and 1991 were combined for analysis. Differences between years (sexes) were checked using analysis of variance (ANOVA), with the day of sampling as a block effect. Relative humidity and moon phase were arcsine transformed to correct for nonnormality of the data.

RESULTS

All bats that were fitted with transmitters were adults except for five juvenile males in August 1990 and one juvenile female in August 1991. Data for body mass and reproductive condition are presented elsewhere (Adam et al. 1994). Transmitters did not appear to adversely affect the bats. Bats showed no difficulty flying upon release and were located at considerable distances from known roosts. During August 1991, two females were captured which had previously been fitted with a transmitter. Masses for these females were not different from the average mass of other females captured during that period. Although transmitters on some bats emitted signals for up to 10 days, we considered 5 days to be the normal life of transmitters in this study. Data from all 60 bats were used, regardless of the life of the transmitters.

Analysis of variance demonstrated no day effect ($F = 2.81$; $df = 4, 20$; $P > 0.10$) and no interaction between day and year ($F = 1.48$; $df = 4, 20$; $P > 0.10$). Activity rates were higher in 1991 than in 1990 ($F = 22.9$; $df = 1, 20$; $P < 0.0001$) (Fig. 1). It is unclear whether this difference was due to sex or varying conditions between summers, as males and females were not tested in both summers.

Bats did not emerge to forage until 30 to 45 minutes post-sunset (Fig. 1). Males in 1990 exhibited a pattern with highest activity during the first few hours of the night (Fig. 1a). The activity of females in 1991 was more sustained throughout the night (Fig. 1b). Females in these periods were either pregnant (May) or lactating (June) (Adam et al. 1994), suggesting the use of night roosts and/or shorter foraging bouts which allowed them to return to the maternity roost to nurse their young.

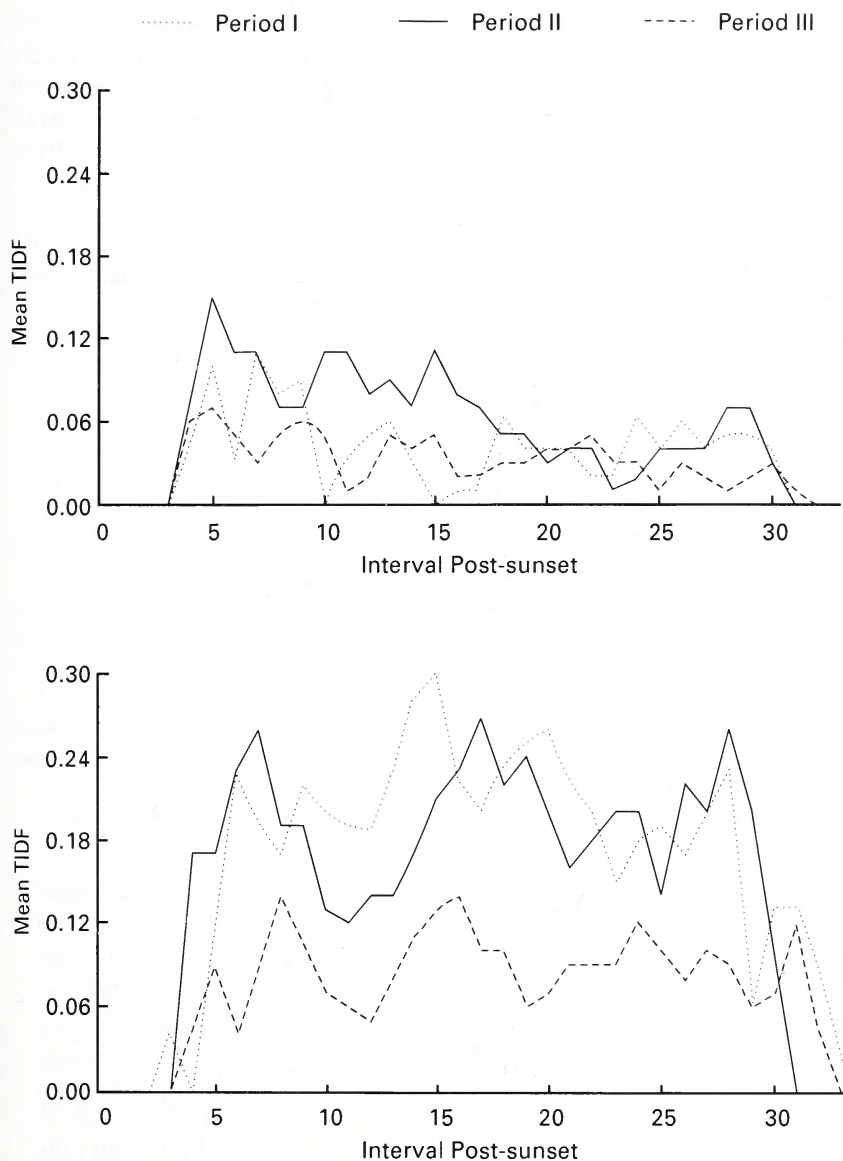


Fig. 1. Mean frequency of detection by 20-minute time intervals (TIDF) post-sunset for *P. t. virginianus* comparing sampling periods; males (a): Period I = June, Period II = July, Period III = August 1990; females (b): Period I = May, Period II = June, Period III = August 1991), Lee County, Kentucky.

Three environmental variables were related to *NDF* (Table 1); *NDF* was positively associated with percent relative humidity, and negatively related to both wind speed and moon phase. Stepwise regression demonstrated a significant ($F = 5.93$, $P = 0.0073$, $R^2 = 0.30$) relationship of *NDF* with relative humidity and moon phase, eliminating wind speed from

Table 1. Regression analyses of mean nightly detection frequency (*NDF*) with environmental variables for *P. t. virginianus*, Lee County, Kentucky, summers 1990 and 1991.

Regression	Environmental variable	Coefficient	SE	P
Simple	Relative humidity	0.23	0.085	0.01
	Moon phase	-0.06	0.026	0.03
	Wind speed	-0.01	0.004	0.04
Multiple	Relative humidity	0.20	0.083	0.02
	Moon phase	-0.05	0.025	0.06

Table 2. Values for nightly detection frequency (*NDF*) and environmental variables for *P. t. virginianus*, Lee County, Kentucky, summers 1990 and 1991.

Variable	Mean	CV	Range	
			High	Low
<i>NDF</i>	0.08	88.5	0.30	0.01
Relative humidity (%)	0.77	11.0	0.97	0.64
Moon phase (%)	0.44	85.2	0.99	0.00
Wind speed (km/hr)	10.80	32.0	20.50	6.40
Barometric pressure (mb)	1,017.00	0.4	1,024.00	1,011.00
Maximum temperature (C)	28.40	12.3	33.30	18.90
Minimum temperature (C)	16.00	19.8	21.10	11.10
Precipitation (cm)	0.61	221.0	5.84	0.00
Prior precipitation ¹ (cm)	0.67	204.0	5.84	0.00

¹ Represents rainfall during the day prior to sampling.

the final model. No pattern was observed between significant and nonsignificant environmental variables using coefficients of variation (Table 2), indicating no bias because of differences in the amount of variability in these sets of variables.

DISCUSSION

We found a direct relationship between flight activity of *P. t. virginianus* and ambient relative humidity, with bats exhibiting reduced activity on nights with lower percent relative humidity. Using mist-net captures as a measure of activity, Lacki (1984) observed a similar pattern for *Myotis lucifugus* and suggested reduction in flight activity as a behavioral mechanism for avoiding water loss on nights when ambient conditions created large vapor pressure deficits.

Bats experience water loss in flight and can lose water because of roost conditions (Carpenter 1969). Substantial water loss accompanies digestion in *M. lucifugus* (Bassett and Wiebers 1980) with water balance in female *M. lucifugus* (Kurta et al. 1989) and female *Eptesicus fuscus* (Kurta et al. 1990) influenced by reproductive condition. Because water loss by bats is dependent on ambient temperature and water vapor pressure under laboratory conditions (Bassett 1980) and water loss increases with higher levels of flight activity (Studier 1970), we suggest that our data support the existence of a behavioral response by bats for avoiding extremes in vapor pressure deficits during flight.

Factors such as prey activity and availability may also contribute to the observed activity patterns, but were not investigated in our study. Data comparing the abundance of insect prey with ambient relative humidity are sparse; however, in one study no association was found between relative humidity and activity of moths (Mizutani 1984). Moths are the predominant item in the diet of *P. t. virginianus* (Sample and Whitmore 1993).

The inverse relationships we observed between activity of *P. t. virginianus* and both moon phase and wind speed are consistent with other findings reported in the literature (O'Farrell et al. 1967, Erkert 1974, Fenton et al. 1977). Whether avoidance of moonlight by *P. t. virginianus* was because of predators or availability of insect prey or both is unclear. Several species of owls were common in the study area, and abundance of insect prey has been shown to be negatively related to moon phase (Anthony et al. 1981). Observations at a maternity colony of a related subspecies, the Ozark big-eared bat (*P. t. ingens*), found no patterns between flight activity and indices of moon brightness (Clark 1991).

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The Pygmy Shrew, *Sorex hoyi winnemana*
(Insectivora: Soricidae), from the Coastal Plain
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ABSTRACT—*Sorex hoyi winnemana* from two counties in extreme northeastern North Carolina represent the first documented specimens of pygmy shrews from the Coastal Plain and the first collected in North Carolina in 50 years. The 15 pygmy shrews were collected from a variety of habitat types, ranging from shrubby-grassy fields in ditched peaty wetlands to managed pine plantations and upland hardwood forests.

The smallest of the North American long-tailed shrews (genus *Sorex*) is *Sorex hoyi*, aptly named the pygmy shrew. At 2–3 g with a total length of 70–86 mm, of which 25–33 mm is tail, the pygmy shrew is the smallest mammal in North Carolina and among the world's smallest mammals. The masked shrew (*Sorex cinereus*) and the southeastern shrew (*S. longirostris*) are similar in appearance and in proportions, but both are somewhat larger (Webster et al. 1985). Besides having slightly longer bodies and tails, *S. cinereus* and *S. longirostris* have five prominent unicuspid, whereas the pygmy shrew has only three distinct unicuspid, the third and fifth being greatly reduced.

The pygmy shrew is distributed throughout the northern tier of states from Minnesota through Maine and extensively in Canada and Alaska, with fingers of distribution extending southward in the Rocky and Appalachian Mountains (Hall 1981), which suggests the animals need boreal conditions. However, studies involving the extensive use of pitfall traps have documented that *S. hoyi* is more widely distributed and occupies a wider range of habitats in the southeastern part of its geographic distribution than it does elsewhere. In Virginia, pygmy shrews have been found in at least 20 counties, including seven counties

west of the Blue Ridge where they were unknown before 1980 (Pagels 1987).

In North Carolina, the pygmy shrew is considered to be rare and of undetermined status (Webster 1987), in part because only three specimens, all from the extreme western mountainous region of the state, have been found. Of these, two specimens are from Bent Creek (23 April 1928), Buncombe County, and the other (6 September 1941) from Newfound Gap in nearby Swain County (Webster 1987).

During extensive studies of the southeastern shrew in the vicinity of the Great Dismal Swamp National Wildlife Refuge (Refuge) of southeastern Virginia and northeastern North Carolina from 1986–91, we collected *Sorex hoyi* from Camden and Gates counties, in extreme northeastern North Carolina. These represent the first documented specimens of *Sorex hoyi* from North Carolina in nearly 50 years, as well as the first of this species from the Coastal Plain (Lee et al. 1982).

METHODS

We used pitfall traps, consisting of #10 metal cans sunk flush into the ground and half-filled with water, to collect small mammals. Pitfall traps are very effective in trapping small cryptic mammals such as shrews (Padgett 1991). These traps offer advantages in that they do not need to be checked daily, are relatively maintenance free, and capture small shrews (and some other species of small mammals) that normally are difficult to collect in other traps. We placed pitfall traps in transects along roads and trails at measured intervals or in 0.25-ha grids spaced 12.5 m apart in 5 × 5 arrays. Each transect or grid was trapped for 3–4 weeks.

One Gates County site was located along Weyerhaeuser Ditch in the Refuge 2 km north of Highway 158, and the other was a transect extending from the escarpment on the western boundary of the Refuge into the swamp. This transect was located 2 km northeast of the intersection of Route 32 and State Route 1332. The Camden County grids were located on a large tract 9 km east–northeast of South Mills.

RESULTS AND DISCUSSION

We collected 15 *Sorex hoyi*, referable to *S. h. winnemana*, during the course of our survey, nine from the southern section of the Refuge in Gates County and six outside the Refuge on three grids in Camden County. Within the Refuge, eight animals were collected from the site adjacent to Weyerhaeuser Ditch. This site was located in an

upland (or mesic) area of the Dismal Swamp locally referred to as "mesic islands"; these are remnant Pleistocene marine deposits oriented in east-west directions. In contrast to the surrounding bottomland forest of tupelo (*Nyssa aquatica*), red maple (*Acer rubrum*), and scattered bald cypress (*Taxodium distichum*), these "island" habitats have such species as American beech (*Fagus grandifolia*), swamp chestnut oak (*Quercus michauxii*), blackgum (*Nyssa sylvatica*), and loblolly pine (*Pinus taeda*). The remaining specimen from the Refuge was collected along the Nansemond (or Suffolk) Escarpment, a Pleistocene feature that delineates the western boundary of the Dismal Swamp, in a transitional wetland forest composed of both upland and bottomland species.

The six pygmy shrews from Camden County were taken in a variety of habitats, all with black peaty loam soils, sometimes with some sand component. Five pygmy shrews came from recently (<2 years) clearcut sites regenerating mostly in mixed grasses and a few shrubs, and one was collected from a 15-year-old loblolly pine plantation with pine straw as virtually the only ground cover.

The specimens from Gates County ranged from 64 to 81 mm (\bar{x} = 75.44 mm), whereas those from Camden County ranged from 78 to 81 mm (\bar{x} = 79.67 mm). In the Gates County specimens, the tails averaged 36% of total length, compares to 33% in the Camden County specimens. Although the sex of some individuals could be determined, we were unable to establish useful sex ratios. Other shrews caught at one or more sites yielding pygmy shrews include the Dismal Swamp southeastern shrew, (*Sorex longirostris fisheri*), the short-tailed shrew (*Blarina brevicauda*) and in Camden County, the least shrew (*Cryptotis parva*).

As is typical of studies using pitfall traps in Virginia (John Pagels, Virginia Commonwealth University and Kurt Buhlman, Virginia Natural Heritage Program, personal communication), the distribution of pygmy shrews appears to be patchy. For example, in Camden County pygmy shrews were caught on three of 10 grids, four on one site, and one on each of the others; seven other sites yielded none. In Gates County in the Refuge, pygmy shrews were taken from two of six sites in habitats that seemed comparable.

We verified that pygmy shrews occur in a range of habitats: we caught shrews in fields in early succession, maturing loblolly pines, and in mature deciduous forest. In the Refuge (Gates County), pygmy shrews were collected on slightly higher and better drained sites than the surrounding more typical Dismal Swamp forested swampland dominated by tupelo, red maple, and bald cypress. The Camden County site is located in the Pasquotank River drainage, and therefore is also

a part of the historic Dismal Swamp, but the land has been ditched, creating slightly drier conditions than probably prevailed there before development. John Pagels (personal communication), who has used pitfall traps in extensive studies in many counties in Virginia, has caught pygmy shrews in many different habitats but not in wetland habitat. In Virginia, Pagels (1987) has collected *Sorex hoyi* with six other soricid shrews, but not with *Blarina*. In conclusion, our studies indicate that in North Carolina, as elsewhere, pygmy shrews have patchy distributions in a range of habitats; they probably occur throughout much more of the state than is presently known.

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Additional Records of the Pygmy Shrew,
Sorex hoyi winnemana Preble (Insectivora: Soricidae),
in Western North Carolina

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ABSTRACT—Additional records of the pygmy shrew, *Sorex hoyi winnemana* Preble, are reported from 14 localities in 7 counties of western North Carolina. Results of recent surveys in adjacent regions of Tennessee and Georgia indicate that the species is widely distributed in the extreme southern Appalachian Mountains, including North Carolina, but is nowhere abundant.

The pygmy shrew, *Sorex hoyi winnemana*, has been regarded as one of the rarest mammals in the southeastern United States. In 1980 (see Diersing 1980, Handley et al. 1980), there were only 17 records known from southern Illinois east to Maryland and south throughout the Appalachian highlands to the Carolinas and Georgia. However, more recently, considerable information on the distribution, abundance, and habitat associations of this species has become available from Indiana (Caldwell et al. 1982, Cudmore and Whitaker 1984), Virginia (Handley et al. 1980, Pagels 1987, Pagels et al. 1992, Mitchell et al. 1993), Kentucky (Caldwell 1980, Caldwell and Bryan 1982), Tennessee (Kennedy et al. 1979, Kennedy and Harvey 1980, Tims et al. 1989, Harvey et al. 1991, Harvey et al. 1992, Feldhamer et al. 1993), South Carolina (Mengak et al. 1987), and Georgia (Wharton 1968). This information indicates that this subspecies can be found over a wider range of habitats and geographic area than previously known. Although nowhere abundant, it may be common where it occurs.

The first North Carolina records of *Sorex hoyi* were of two individuals collected by A. H. Howell and reported by Jackson (1928) from Bent Creek Experimental Forest in Pisgah National Forest, Buncombe County. Webster (1987) indicated that the Buncombe County specimens were erroneously reported from Transylvania County by Smith et al. (1960),

Diersing (1980), and Lee et al. (1982). However, a single specimen was subsequently collected in Transylvania County, at Cedar Mountain, and reported by Mengak et al. (1987). Additionally, Hoffmeister (1968) reported a single specimen from Newfound Gap, Swain County. Thus, until recently the species was represented by only four specimens from North Carolina.

In August 1993 E. v. d. Berghe (Appalachian Environmental Research Center, Frostburg, Maryland) submitted to J. L. collections of shrews that were made in North Carolina as incidental captures in surveys for carabid beetles. Included in these collections were two *Sorex hoyi* from McDowell County and an additional specimen from Graham County. Subsequently, we obtained a record of an additional specimen from M. Steele (Wilkes University, Wilkes Barre, Pennsylvania), who recovered *S. hoyi* from Mount Mitchell, Avery County, in pitfall studies for sorcid parasites.

In this volume, Padgett and Rose (1994) report on significant new records of *S. hoyi* from the Dismal Swamp area in the extreme northeastern portion of North Carolina. Because the species is listed as special concern in North Carolina by the North Carolina Wildlife Resources Commission (see also Webster 1987), additional information on its distribution is needed. We report on new records of this species and the results of preliminary surveys to document additional records in western North Carolina.

METHODS

To document the occurrence of *S. hoyi* in regions from which it had not previously been reported, we established pitfall traplines at eleven sites in Clay, Cherokee, Jackson, and Macon counties in extreme western North Carolina from December 1993 through January 1994. Additionally, we established 15 pitfall trap lines at Coweeta Hydrological Laboratory along an altitudinal gradient from 710 m to 1,525 m from April through May 1994.

Traplines consisted of twenty, 32-ounce plastic cups (11-cm lip diameter, 14-cm depth) placed flush with or below the surface of the ground and adjacent to rotting logs, stumps, rocks, or other forest floor debris. Pitfalls were placed approximately 10-m apart along a linear transect and were set in a diversity of typical southern Appalachian forest habitats and checked biweekly. Because the species is protected in North Carolina, we were required to discontinue trapping after the second record of *S. hoyi* was obtained at a site.

RESULTS AND DISCUSSION

Our survey of 13,200 trap nights yielded 10 records of *Sorex hoyi*: one each from Cherokee, Clay, and Jackson counties and seven from Macon County. Five of the Macon County records were obtained at Coweeta Hydrological Laboratory. The western North Carolina sites ranged in elevation from 700 m to 1,524 m in a variety of moderate to mesic hardwood to mixed hardwood-pine sites. *Sorex hoyi* was taken in a heath bald dominated by rhododendron (*Rhododendron maximum*); cove hardwood communities dominated by yellow poplar (*Liriodendron tulipifera*), northern red oak (*Quercus rubra*), white oak (*Q. alba*), and buckeye (*Aesculus octandra*); moderately xeric sites dominated by white oak, northern red oak, hickory (*Carya* spp.), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), and white pine (*Pinus strobus*); and streamside communities dominated by eastern hemlock (*Tsuga canadensis*) and rhododendron. Standard body measurements for the 13 new North Carolina specimens available to us are as follows: total body length (\bar{x} = 68.7 mm, range = 65.0–73.5 mm), tail length (\bar{x} = 26.2 mm, range = 24.0–28.4), and hind foot length (\bar{x} = 8.0, range = 7.0–8.5 mm).

The few historical collection records of this species from western North Carolina probably do not necessarily reflect its rarity in the area but rather inappropriate collecting methodology. In the past 10–12 years significant information regarding this species has become available, largely through pitfall trapping, which has been shown to be the most (if not the only) effective method of collecting insectivores (Handley and Kalko 1993). Trapping efforts by Harvey et al. (1991) in the southern districts (Monroe and Polk counties) and Harvey et al. (1992) in the northern districts (Unicoi, Johnson, and Carter counties) of the Cherokee National Forest, Tennessee, have indicated *S. hoyi* to be widely distributed but nowhere abundant. Harvey et al. (1991) reported 16 captures in 226,054 pitfall trap nights in a diversity of forest habitats in the southern portions of the Cherokee National Forest ranging in elevation from 396 m to 1,122 m. Harvey et al. (1992) report 13 captures in 389,995 pitfall trap nights in a similar diversity of forest habitats in the northern portions of the Cherokee National Forest ranging in elevation from 695 m to 1,524 m. Similarly, in 67,500 pitfall trap nights we have recorded 72 *S. hoyi* from 42 localities throughout the entire Blue Ridge Province of Georgia where the species is widely distributed in a variety of forest habitat types, including clearcuts, early and mid-successional forest stages, as well as mature stands in streamside, xeric, and mesic communities at elevations ranging from 700 m to 1,372 m. In Georgia, it is nowhere abundant, but is widely distributed.

COLLECTION RECORDS

Records of *Sorex hoyi* from western North Carolina using acronyms for the museum collections in which the specimens are housed follow Yates et al. (1987).

Avery Co.: Mount Mitchell (1, M. Steele Collection). *Buncombe Co.*: Bent Creek Experimental Station, Pisgah National Forest (2, USNM). *Cherokee Co.*: Nancy Gap (2, UGAMNH). *Clay Co.*: 3.0 mi. E. Fires Creek Recreation Area (1, UGAMNH). *Graham Co.*: 15 mi. NW Robbinsville, Joyce Kilmer Memorial Forest (1, UGAMNH). *Jackson Co.*: 4.5 mi. S Cashiers (1, UGAMNH). *Macon Co.* 3.0 mi. W. Highlands (1, UGAMNH), 0.5 mi. E. Winding Stair Gap on U.S. 64 (1, UGAMNH); Albert Mt., Coweeta Hydrological Laboratory (1 UGAMNH); Cold Spring Gap, Coweeta Hydrological Laboratory (1 UGAMNH); Cold Spring Cove, Coweeta Hydrological Laboratory (1 UGAMNH); Lick Branch, Coweeta Hydrological Laboratory (2 UGAMNH). *McDowell Co.*: Balsam Gap, along Blue Ridge Parkway at mile marker 357 (1, UGAMNH); Glassmine Falls, along Blue Ridge Parkway at mile marker 362 (1, UGAMNH). *Swain Co.*: Newfound Gap (1, UGAMNH). *Transylvania Co.*: Cedar Mountain (1, CUVVC).

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Food and Ectoparasites of the Southern Short-tailed
Shrew, *Blarina carolinensis* (Mammalia: Soricidae),
from South Carolina

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ABSTRACT—Food habitats and ectoparasites were examined in a sample of 50 individuals of *Blarina carolinensis* collected in a hardwood forest on the Coastal Plain of western South Carolina. Both in terms of volume and frequency of occurrence, predominant foods were slugs and snails (Mollusca), the hypogeous fungus *Endogone*, earthworms (Annelida), and beetle (Coleoptera) adults and larvae. Ectoparasites observed on *B. carolinensis* included one species of flea (*Doratomyss blarina*), one species of beetle (*Leptinus americanus*), and 25 species of mites, the most frequent being *Orycteroxenus soricis*, *Asiochirus blarina*, *Echinonyssus blarinae*, *Haemogamasus liponyssoides*, and several species of *Pygmephorus*.

A good deal of information exists on the foods and ectoparasites of the northern short-tailed shrew, *Blarina brevicauda* (Say 1823); however, this is not the case for the southern short-tailed shrew, *B. carolinensis* (Bachman 1837). We are not aware of any detailed information on the foods eaten by *B. carolinensis*, and know of only five species of ectoparasites that have been reported: the laelapids *Androlaelaps fahrenheitsi* and *Haemogamasus harperi* by Hayes and Guyton (1958), *Eulaelaps stabularis* by Hayes and Guyton (1958) and Jameson (1947), and *Myonyssus jamesoni* by Ewing and Baker (1947),

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and the myobiid *Blarinobia simplex* by Ewing (1938). The purpose of this paper is to present data on the food habits and ectoparasites of *B. carolinensis* from South Carolina, and to compare these with data that have been reported for *B. brevicauda*.

MATERIALS AND METHODS

Shrews were collected over a 21-day period in May 1986 from the Savannah River Ecology Laboratory's Mill Creek small mammal trapping grid. The Mill Creek grid is located in a mixed hardwood cove forest located on the United States Department of Energy's Savannah River Site, near Aiken, South Carolina, and is on the western-most Coastal Plain of the State; specifics of grid dimensions and habitat structure have been described elsewhere (Gentry et al. 1968, 1971). One Museum Special and one Victor mouse trap were set at each station of the grid; traps were baited with peanut butter and checked daily. Captured shrews were placed in individual plastic bags and frozen for later examination.

Stomach contents of each animal were removed and then identified under a dissecting microscope. The volume of each item in each stomach was estimated visually. Data were compiled as percent frequencies (percentage of shrews with each item) and percent volumes (average percentage of each food) of each item observed in the entire sample.

We collected ectoparasites by examining the fur with a dissecting microscope. When ectoparasites were observed to occur in relatively small numbers, all individuals were collected; when the numbers of ectoparasites were large, the numbers individuals of each species were estimated, and samples were taken of each. Data on food habits and ectoparasites were compared to similar data for *B. brevicauda* from Indiana (Mumford and Whitaker 1982). Shrews from Indiana were collected from a variety of habitats.

RESULTS

FOODS

Forty-five of the 50 individuals of *B. carolinensis* examined contained food, totaling 23 items (Table 1). The five dominant foods were slugs and snails (18.5% of total volume), the hypogenous fungus *Endogone* and related genera (16.3%), earthworms (14.8%), unidentified adult beetles (9.6%), and unidentified beetle larvae (5.8%). Total volumes of Coleoptera, Lepidoptera, and Diptera were 17.8, 6.0, and 6.7%, respectively. No single food item clearly was dominant in the sample of *B. carolinensis*; slugs and snails, *Endogone*, and earthworms were

Table 1. Food items observed in the stomachs of 45 short-tailed shrews (*Blarina carolinensis*) from South Carolina and 125 *B. brevicauda* from Indiana (Mumford and Whitaker 1982).

	<i>B. carolinensis</i>		<i>B. brevicauda</i>	
	Volume	Frequency	Volume	Frequency
Slugs and snails	18.0	26.8	8.5	14.4
<i>Endogone</i> (and related genera)	16.3	29.3	3.6	11.2
Earthworms	14.8	22.0	37.5	48.1
Coleoptera adults	9.6	19.5	4.2	7.2
Coleoptera larvae	5.8	24.4	4.0	7.2
Spider	4.6	9.8	0.5	2.4
Lepidoptera larvae	3.7	7.3	8.2	16.8
Unidentified larvae	3.6	4.9	0.3	1.6
Diptera adults	3.0	4.9	0.3	1.6
Phalangida	2.4	2.4		
Scarabaeidae larvae	2.4	2.4	0.8	0.8
Lepidoptera adult	2.3	2.4	0.1	0.8
Cricket	2.1	4.9	6.2	8.8
Tipulidae	2.1	2.4		
Unidentified	1.8	9.8		
Muscoid Diptera	1.6	2.4	0.8	0.8
Hemiptera	1.3	4.9	1.0	2.4
Vegetation	1.2	2.4	2.2	11.2
Insect	1.1	2.4	3.8	14.4
Vertebrate	1.0	2.4	0.3	0.8
Formicidae	0.6	4.9	0.5	4.5
Chilopoda	0.5	2.4	4.5	8.0
Hemerobiidae	0.1	2.4		
Carabidae			2.7	4.0
Dipterous larvae			1.8	5.6
Isopoda (sowbugs)			1.6	1.6
Pentatomidae			1.4	3.2
Scarabaeidae			1.1	3.2
<i>Elymus</i> seeds			0.8	0.8
Coleoptera: pupae			0.8	0.8
Acrididae			0.8	0.8
Orthoptera: internal organs			0.7	0.8
Plecoptera			0.6	0.8
Curculionidae			0.6	1.6
Mast			0.6	1.6
Gryllacrididae			0.4	0.8
Enchytraeidae			0.2	0.8
Syrphidae			0.2	0.8
Cicadellidae			0.1	0.8
Staphylinidae			0.1	0.8

represented about equally and collectively comprised about half of the food in the sample. Whereas no food item was dominant in the sample of *B. carolinensis*, earthworms clearly were dominant (37.5% volume) in *B. brevicauda*, followed by slugs and snails (8.5%), lepidopterous larvae (8.2%), Gryllidae (6.2%), and Chilopoda (4.5%) (Table 1).

ECTOPARASITES

Ectoparasites were observed on all *B. carolinensis* examined, and individuals of 27 different species were collected (Table 2): one species of flea (*Doratomyssa blarina*), one species of beetle (*Leptinus americanus*), and 25 species of mites from eight families (Acaridae, Anoetidae, Cyrtolaelapidae, Laelapidae, Listrophoridae, Myobiidae, Pygmephoridae, and Trombiculidae). Both in terms of the percentage of hosts infested and the mean numbers observed per host, the most frequently observed ectoparasites on *B. carolinensis* were *Echinonyssus blarinae*, *Haemogamasus liponyssoides* (Laelapidae), *Asiochirus blarina* (Listrophoridae), *Orycteroxenus soricis* (Acaridae), and *Protomyobia blarinae* (Myobiidae).

Doratomyssa blarina, the only flea observed on *B. carolinensis*, was the second most abundant of the six flea species observed on *B. brevicauda*. The acarid mite *Orycteroxenus soricis* occurred on both species of shrew, but two acarid hypopi, *Xenoryctes latiporus* (only on *B. carolinensis*) and *Dermacarus hypudaei* (only on *B. brevicauda*), also were present. *Asiochirus blarina* was the only listrophorid collected; it occurred on both species of shrew. Five species of laelapid mites were collected from *B. carolinensis*, as compared to eight species on *B. brevicauda*. The laelapid species *Haemogamasus liponyssoides* was one of the two most abundant ectoparasites on both species of shrew. *Echinonyssus blarinae* was more abundant on *B. carolinensis*, whereas *Androlaelaps fahrenheitsi* was the most abundant laelapid on *B. brevicauda*. Seven species of *Pygmephorus* were collected from *B. carolinensis*, and 12 species from *B. brevicauda*.

Of the 11 species of pygmephorids observed on *B. carolinensis*, four were in the genus *Bakerdania*, a genus that was not observed on *B. brevicauda*. Three species of *Bakerdania* probably are undescribed. Thirteen species of ectoparasite (1 flea, 1 beetle, 11 mite species) were common to both species of *Blarina*. Fourteen species of ectoparasites were observed only on *B. carolinensis*: these 14 consisted of one laelapid, one acarid, eight species of pygmephorids, two cyrtolaelapids, an anoetid, and a chigger (Trombiculidae). Of the 32 species reported for *B. brevicauda*, 19 were found only on that host. The 19 consisted

on five species of fleas, four species of laelapid mites, one species of acarid mite, and a species of *Pygmephorus*.

DISCUSSION

Both *B. carolinensis* and *B. brevicauda* eat a wide variety of foods: 23 categories of food items in the South Carolina material ($n = 45$), compared with 36 categories in the much larger sample of *B. brevicauda* ($n = 125$) from Indiana. The lower percent volume of earthworms observed for *B. carolinensis* likely represents the low numbers of earthworms that are supported by the sandy soils of the Savannah River Site, rather than a difference in dietary preference between *B. carolinensis* and *B. brevicauda*.

The hypogeous mycorrhizal fungus *Endogone* was one of the more heavily eaten foods in the shrews from South Carolina at 16.3% of the volume, but formed only 3.6% of the total volume in the foods of Indiana shrews. *Endogone* (including related genera, see Castellano et al. 1989) often is important as a food of small mammals (Whitaker 1962, Williams and Finney 1964). The small mammal-fungal relationship is an important component of many communities because small mammals act as dispersal agents for mycorrhizal fungi (Maser et al. 1978).

Of the five ectoparasitic species that previously had been reported from *B. carolinensis*, all were found during our study (marked with asterisks, Table 2) except for *Haemogamasus harperi*. The flea most frequently observed on *B. brevicauda*, *Ctenophthalmus pseudagyrtis*, was not collected from *B. carolinensis*; however, *C. pseudagyrtis* does occur on the Savannah River Site, and has been observed on eastern moles, *Scalopus aquaticus* (G. D. Hartman, unpublished data). The most abundant mites on *Blarina* tend to be the tiny *Asiochirus blarina* (Listrophoridae) and hypopi of *Orycterxenus soricis* (Acaridae); both of these ectoparasites likely were more abundant than the data indicate.

The number of ectoparasite species observed on *B. carolinensis* was less than for *B. brevicauda*, in part because of the smaller number of *B. carolinensis* examined. However, in spite of the different sample sizes, there were notable differences between the ectoparasite assemblages. Of 27 species observed on *B. carolinensis*, 14 were found only on this host, and of the 32 species reported for *B. brevicauda*, 19 were found only on that host. Anotids, cyrtolaelapids, trombiculids, and the genus *Bakerdania* (Pygmephoridae) were observed only on *B. carolinensis*. Although the species of *Pygmephorus* found on the two host species were not similar, this is not too surprising because pygmephorid mites that occur on mammals are not host specific.

Table 2. Ectoparasites from 50 individuals of *Blarina carolinensis* from South Carolina compared with those from 92 of *B. brevicauda* from Indiana (Mumford and Whitaker 1982).

Ectoparasite Taxon	<i>B. carolinensis</i>			<i>B. brevicauda</i>	
	Number	Percent ¹	Number	Percent	\bar{x}
SIPHONAPTERA (fleas)					
<i>Ctenophthalmus pseudagyrtes</i> Baker				15.2	0.32
<i>Doratomylla blarinae</i> Fox	9	18.0	12	7.6	0.18
<i>Eptedia wenmanni</i> (Rothschild)				3.3	0.04
<i>Stenoponia americana</i> (Baker)				1.1	0.02
<i>Corrodopsylla hamiltoni</i> (Traub)				1.1	0.01
<i>Orchopeas howardii</i> (Baker)				1.1	0.01
COLEOPTERA (beetles)					
<i>Leptinus americanus</i> LeCont	1	2.0	1	4.3	0.05
ACARINA (mites and ticks)					
LAELAPIIDAE					
<i>Echinonyssus blarinae</i> (Herrin)	32	64.0	218	1.1	0.01
<i>Haemogamasus liponyssoides</i> Ewing	26	52.0	65	10.9	0.30
* <i>Androlaelaps fahrenheitzi</i> (Berlese) ³	13	26.0	20	23.9	0.70
* <i>Eulaelaps stabularis</i> (Koch)	7	14.0	9	7.6	0.08
* <i>Myonyssus jamesoni</i> Ewing and Baker				2.2	0.30
<i>Haemogamasus longitarsus</i> (Banks)				1.1	0.05
<i>Laelaps kochi</i> Oudemans				1.1	0.01
<i>Androlaelaps casalis</i> (Berlese)	1	2.0	1		
<i>Haemogamasus ambulans</i> (Thorell)				1.1	0.01
<i>Orycterxenus soricis</i> (Oudemans)	24	48.0	102	15.2	13.50
<i>Xenoryctes latiporus</i> Fain and Whitaker	11	22.0	25		
<i>Dermacarus hypudaei</i> (Koch)				1.1	0.01
LISTROPHORIDAE					
<i>Asiochirus blarina</i> Fain and Hyland	26	52.0	127	15.2	28.40

MYOBIIDAE

Protomyobia blarinae Lukoschus et al.**Blarinobia simplex* (Ewing)

PYGMEPHORIDAE

Pygmephorus johnstoni Smiley and Whitaker*P. horridus* Mahunka*P. tamias* Mahunka*P. whartoni* Smiley and Whitaker*P. whitakeri* Mahunka*P. hamiltoni* (near) Smiley and Whitaker*P. rackae* Smiley and Whitaker*P. scalopi* Mahunka*P. designatus* Mahunka*P. equitrichosus* Mahunka*P. moreohorridus* Mahunka*P. faini* Smiley and Whitaker*P. spinosus* Kramer*P. brevicauda* Smiley and Whitaker*P. hastatus* Mahunka*Bakerdania plurisetosa* Mahunka*Bakerdania* sp.

(3 species, probably all new)

CYRTOLAEALAPIDAE

Cyrtolaelaps sp.*Euryparasitus* sp.

ANOETIDAE

Prowichmannia spinifera (Michael)

TROMBICULIDAE (chiggers)

Comatacarus americanus Ewing

19	38.0	141	2.80	3.3	0.14
5	10.0	8	0.20	3.3	0.03
4	8.0	6	1.10	(3) ⁴	
13	26.0	25	0.50	(6)	
10	20.0		0.40		
18	36.0		0.50		
1	2.0	1	0.02	(4)	
15	30.0	34	0.70	(27)	
				(16)	
				(5)	
				(3)	
				(2)	
2	4.0	2	0.04	(2)	
				(1)	
				(1)	
				(1)	
5	10.0	6	0.10		
4	8.0	6	0.10		
16	32.0	28	0.60		
1	2.0	1	0.02		
11	22.0	15	0.30		
14	12.0	6	0.30		

¹Percentage of hosts infested. ²Mean number per host (not per infested host). ³Ectoparasitic species previously reported from *B. carolinensis* are marked with an asterisk. ⁴Values for the numbers of individuals of *Pygmephorus* from Indiana (in parentheses) are numbers actually identified from that host, not the number estimated or counted; the numbers taken were much larger.

CONCLUSION

We report the first study of the food habits of *B. carolinensis*, and we increased, by more than five-fold, the number of species of ectoparasites known to occur on this shrew. However, the specimens of *B. carolinensis* that we examined were collected from a single locality in less than one month. Further studies on *B. carolinensis* from different localities, habitats, and times of the year are needed to account for any temporal or spatial variation in food habits and the occurrence of ectoparasitic species, and to further elucidate the differences or similarities between *B. carolinensis* and *B. breviceauda* in their food habits and ectoparasite assemblages.

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Mensural Discrimination of Four Species of *Peromyscus* (Rodentia: Muridae) in the Southeastern United States

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ABSTRACT—We subjected 17 mensural characters from a total of 460 cotton mice (*Peromyscus gossypinus*), white-footed mice (*P. leucopus*), deer mice (*P. maniculatus*), and old-field mice (*P. polionotus*) to discriminant analysis to maximally distinguish among specimens of these species in the southeastern United States. If external measurements are available, 13 characters are necessary to correctly classify all specimens. If external measurements are not available, 14 cranial characters discriminate at most 91% of the specimens. In pairwise comparisons using external and skull measurements, at least 98% of specimens can be separated with one or two characters. In pairwise comparisons (except *P. leucopus*–*P. maniculatus*) using only skull measurements, at least 95% of specimens can be correctly identified to species with one or two characters. For *P. leucopus* and *P. maniculatus*, six characters correctly separate 86% of the specimens, and two characters separate 82%.

White-footed mice (*Peromyscus*, Golger) are among the most widely distributed and ubiquitous North American mammals (Hall 1981), are the most broadly studied native mammals (King 1968), and are represented extensively in systematic collections. Despite their commonness and familiarity to most biologists, it is still difficult to distinguish among species when we use morphological characters (Hooper 1968). Much literature has resulted from regional attempts to provide for mensural discrimination among *Peromyscus*, especially between and within Osgood's (1909) *maniculatus* and *leucopus* species-groups. Papers have been published separating the white-footed mouse (*P. leucopus* [Rafinesque]), from the deer mouse (*P. maniculatus* [Wagner]) in New England (Choate 1973), Kansas (Choate et al. 1979), Wisconsin (Stromberg 1979), and Maryland (Feldhamer et al. 1983); separating the white-footed mouse from the cotton mouse (*P. gossypinus* [Le Conte]), in Alabama (Linzey et al. 1976) and eastern Texas (Engstrom et al.

1982); separating five *Peromyscus* species in New Mexico (Smart 1978); and separating four *Peromyscus* species in Arkansas (McDaniel et al. 1983). These studies indicate that it is usually possible to distinguish between morphologically similar species, but the characters necessary to do so vary geographically. Thus, for example, the characters used to distinguish between *P. leucopus* and *P. maniculatus* in New England differ from those in Wisconsin or Kansas. This almost ad hoc approach

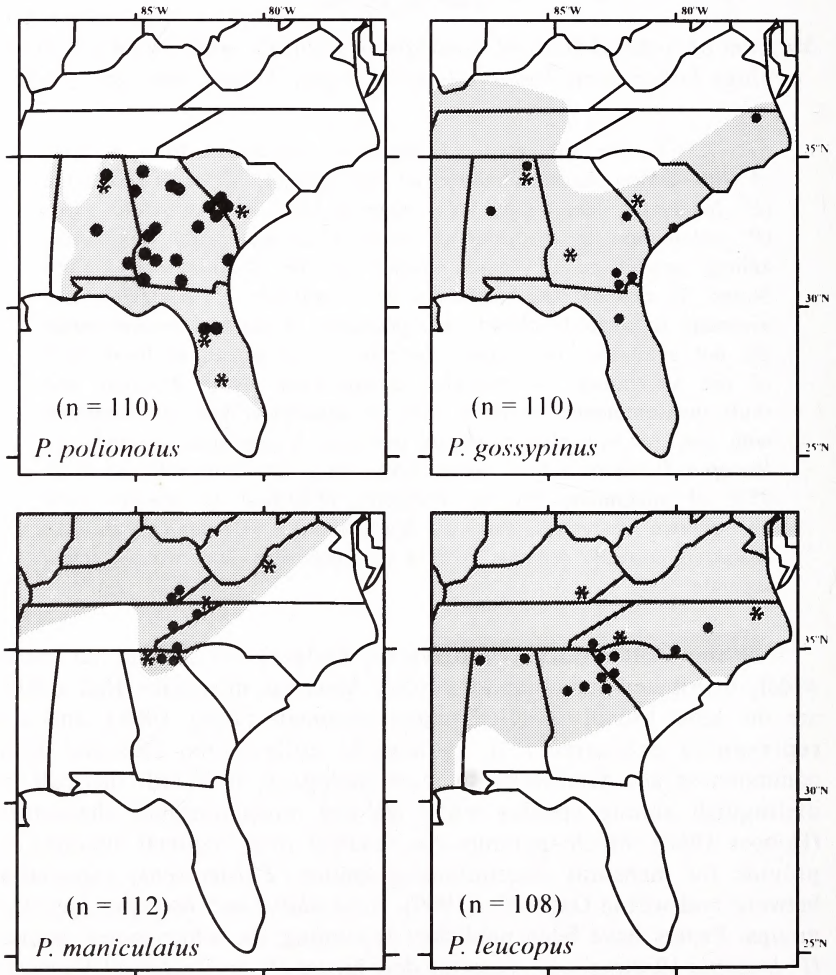


Fig. 1. Southeastern distribution of the four *Peromyscus* species showing collection location of the specimens used to build the model (•) and specimens used to test the model (*).

to the problem has been necessary because several of the species, particularly *P. leucopus* and *P. maniculatus*, have a high degree of intraspecific variation in morphology.

In the southeastern United States the ranges of four species overlap (Fig. 1). It is difficult to correctly identify these species using available taxonomic keys (e.g., Golley 1962, 1966; Blair et al. 1968; Hall 1981) based only on pelage features and/or cranial measurements. The four species usually can be distinguished based on collection location, habitat, and morphological data. Populations of *Peromyscus maniculatus* in this region are referred to as *P. m. nubiterrae* and are typically found in mesic forests at elevations higher than 900 m, and *P. maniculatus* usually has a sharply bicolored tail that is longer than the head and body. *Peromyscus gossypinus* is generally found in hardwood river bottoms and coastal oak-palmetto (*Quercus* sp. and *Serenoa repens*) forests and is the largest and heaviest of the four species. *Peromyscus polionotus* is generally found in areas of sandy soil and has a very short, distinctly bicolored tail. *Peromyscus leucopus leucopus* is generally found at elevations below 900 m in relatively xeric woodlands. Its tail is shorter than the head and body, and it is smaller and lighter in mass than *P. gossypinus*. A plot of principal component scores generated from the correlation structure of three standard external measurements (body, tail, and hind foot lengths) illustrates the overlap in measurements from specimens collected in the Southeast and graphically illustrates the difficulty in separating these four species based on these features (Fig. 2).

For museum personnel that acquire poorly curated public or private collections, or who desire to reexamine their holdings, identification of specimens from regions where ranges overlap may be difficult. The objective of this study is to examine the effectiveness of statistical procedures to distinguish these species in the southeastern United States without the use of collection-location information and without using statistically unsound ratios (Humphries et al. 1981). To do this, we generate discriminant functions from both external and skull measurements and from skull measurements alone.

METHODS

We used univariate and multivariate statistics to examine 460 *Peromyscus* museum specimens collected in the southeastern United States for variation in 17 morphometric characters. We selected sample sites based on the availability of large numbers of adult specimens from throughout the region. Sample sites were selected to reduce potential for incorrect a priori species identification by eliminating, to some degree, consideration of localities where ranges overlap. These criteria resulted in the distribution of sample sites in Figure 1.

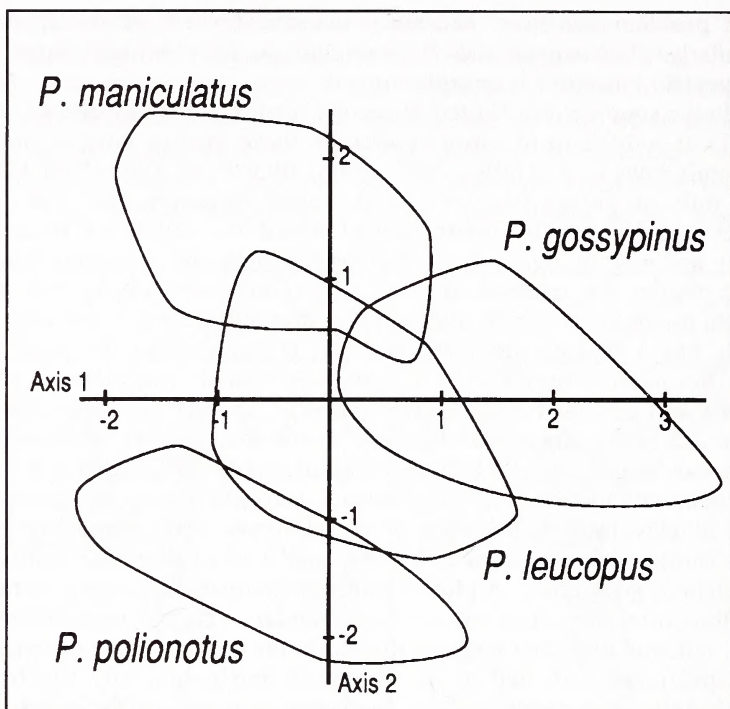


Fig. 2. Distribution of principal component scores generated from external measurements (body, tail, and hind foot lengths) illustrating overlap in the measurements of these characters.

A priori identifications were based on specimen tag information. We used only specimens we believed were correctly identified. We wanted to create a robust generalized model, but we also wanted to build the model based on, as much as possible, animals that we felt were correctly identified. The selection procedure resulted in using 110 *P. gossypinus*, 108 *P. leucopus*, 112 *P. maniculatus*, and 110 *P. polionotus*. The Appendix lists specimens examined. We used five additional specimens of each species, generally selected from locations not included in the model building process, to test the model.

One of us (JL) measured 14 cranial characters to the nearest 0.1 mm with dial calipers and recorded three external measurements from specimen tags. We estimated age from pelage characters (no juvenile gray), tooth wear (significant wear on all major cusps), and degree of cranial suture fusion. We measured only adults (in age classes 4–6 of Schmidly 1973) and excluded specimens with missing data from all analyses. Mensural characters (Choate et al. 1973, DeBlase and Martin

1981) included: head and body length (body), tail length (tail), hind foot length (foot), greatest skull length (SL), basonasal length (BNL), rostral breadth (RB), nasal length (NL), interorbital constriction (OC), zygomatic breadth (ZB), bony palate length (PL), maxillary toothrow length (MTL), total toothrow length (TTL), palatal width (PW), pterygoid breadth (PB), bullar depth (BD), and anterior palatal (incisive) foramen length (PFL). We measured rostral length (RL) from the anteriormost point of the nasals to the anterior edge of the zygomatic arch. Body length was calculated as the difference between total and tail lengths. We excluded ear length due to predominance of missing data.

We performed statistical analyses with Systat 5.1a (Wilkinson 1989) and SPSS 4.01 (Norusis 1990). We tested normality and homogeneity of variance by inspecting plotted residuals and by Bartlett's test for homogeneity of group variances, respectively. Differences among adult age classes and between sexes were tested with analysis of variance, and type I error rates were corrected with the Bonferroni adjustment (Rice 1989). We classified taxa using stepwise discriminant analysis. Variables were included in the models based on minimizing residual variance, prior probabilities were equal to sample size, and varimax rotation was employed. Stepwise discriminant analysis will find an optimal solution based on the data; however, depending on where the analysis begins (i.e., which variables enter the model first), it may find a local, rather than the global, optimum. To help avoid this optimization problem, we removed variables that entered the model in the first steps and repeated the analysis. In one case, that of discrimination based on all external and skull measurements, we found that bullar depth (BD) forced the model onto a local optimum. Therefore, we eliminated this character from further consideration in that model. We used stepwise discriminant analysis to produce two main predictive functions from the smallest set of characters needed to separate all four species—one for external and skull measurements and another for skull measurements alone. In addition, we generated predictive functions that used only one or two measurements to separate in pairwise comparisons among species.

We performed all analyses on raw data without transformation (because transformation did not result in homogeneous variances) and without removing size (Burnaby 1966, Rohlf and Bookstein 1987) because this produced the simplest tool for the identification of questionable specimens in the future. Although there was significant heterogeneity of variances among species for some characters, standard transformations (e.g., logarithm, etc.) did not homogenize it, and raw data were more effective in discrimination than log-transformed data.

Table 1. Mean, standard error, and range of 17 external and cranial measurements (mm) of four *Peromyscus* species in the southeastern United States.

Character	<i>P. gossypinus</i>			<i>P. leucopus</i>			<i>P. maniculatus</i>			<i>P. polionotus</i>			
	\bar{x}	SE	Range	\bar{x}	SE	Range	\bar{x}	SE	Range	\bar{x}	SE	Range	
Body	99.5	0.74	82-133	87.6	0.65	73-106	86.3	0.68	71-102	75.7	0.62	59-99	
Tail	73.1	0.58	58-91	65.1	0.66	49-83	88.3	0.68	71-106	45.1	0.37	36-53	
Foot	22.1	0.09	20-24	19.4	0.09	16-21	20.1	0.10	16-22	16.8	0.10	13-20	
Greatest skull length (SL)	27.9	0.09	25.8-29.9	25.2	0.07	23.0-27.1	24.6	0.07	22.8-27.0	22.2	0.07	20.1-23.9	
Basoanal length (BNL)	25.2	0.10	22.6-28.4	22.6	0.08	20.7-24.4	22.0	0.07	20.0-23.7	19.8	0.07	17.5-21.6	
Rostral length (RL)	9.0	0.05	7.8-10.4	7.6	0.03	26.8-8.5	7.7	0.04	6.6-8.8	6.8	0.04	5.8-7.8	
Greatest rostral breadth (RB)	3.2	0.02	2.8-3.6	3.0	0.02	2.6-3.4(3.8) ¹	2.9	0.02	2.5-3.3	2.8	0.02	2.4-3.1(3.7)	
Nasal length (NL)	11.0	0.06	9.5-12.2	9.7	0.05	8.5-11.0	9.6	0.04	8.3-10.5	8.6	0.05	7.4-9.5	
Interorbital constriction (OC)	4.4	0.01	4.0-4.7	4.1	0.02	3.7-4.7	3.9	0.02	3.2(2.8)-4.4	3.7	0.02	3.3-4.1(4.8)	
Zygomatic breadth (ZB)	14.1	0.06	12.9-15.7	12.9	0.04	12.0-13.9	12.6	0.04	11.6-13.8	11.7	0.04	10.8-12.7	
Bony palate length (Palatilar) (PL)	11.1	0.05	9.9-12.6	9.9	0.04	8.9	10.8	9.7	0.03	8.8-10.7	8.7	0.04	7.4-9.9
Maxillary toothrow length (MTL)	3.8	0.02	3.4-4.1	3.4	0.02	3.0-3.8	3.4	0.01	3.1-3.9	3.1	0.02	2.6-3.5	
Total toothrow length (TTL)	12.7	0.04	11.7-13.7	11.5	0.03	10.5-12.3	11.2	0.03	10.4-12.1	10.1	0.03	9.3-10.8	
Palatal width (PW)	3.0	0.01	2.7-3.3	2.7	0.02	2.4-3.1	2.6	0.01	2.3-3.0	2.5	0.01	2.2-2.9	
Pterygoid breadth (PB)	1.5	0.02	1.0-1.7	1.3	0.01	0.8-1.6	1.2	0.01	1.0-1.5	1.2	0.01	1.0-1.4(1.5)	
Bullar depth (depth of skull) (BD)	9.5	0.03	8.5-10.3	8.8	0.03	8.1-9.6	8.4	0.03	7.8-9.0	8.1	0.03	7.4-8.9	
Ant. palatal foramen length (PFL)	5.6	0.03	4.7-6.3	4.7	0.03	4.0-5.4	4.7	0.02	3.9-5.2	4.1	0.02	3.6-4.7	

¹ Extreme measurements, those greater than five standard deviations from the mean, are shown in parentheses.

RESULTS

In univariate tests, we found significant differences between the sexes in *P. gossypinus* for body length ($P \leq 0.02$), RL ($P \leq 0.02$), and NL ($P \leq 0.05$); in *P. leucopus* for foot ($P \leq 0.03$) and PFL ($P \leq 0.04$); in *P. maniculatus* for SL ($P \leq 0.05$), PB ($P \leq 0.04$), and PFL ($P \leq 0.01$); and in *P. polionotus* for body length ($P \leq 0.01$). Although these differences were individually significant, there was considerable overlap in character ranges, and none was significant when we applied the Bonferroni correction (table-wide significance began at $P \leq 0.003$). The differences between the sexes of *P. maniculatus* approached significance ($P \leq 0.07$), but none was significantly different ($P \leq 0.05$) when subjected to two group (i.e., male vs. female) discriminant analysis. We included gender in the discriminant analysis of all characters, but its effect was not significant, and it did not enter the final stepwise model. Table 1 contains means, ranges, and standard errors for all characters.

Univariate analyses were marginally successful in identifying the four species, but no single measurement unambiguously separated them. Most characters separated the large *P. gossypinus* from the small *P. polionotus*, but six of 17 characters showed overlapping distributions. Tail length greater or less than 55 mm is the simplest method to separate these two species. No single character could separate *P. gossypinus* from *P. leucopus* or *P. maniculatus*, but anterior palatal foramen length 5.4 mm identified most (67%) *P. gossypinus*. Tail length 83 mm separated 81% of *P. maniculatus* from the other three species, but four *P. gossypinus* had tails longer than 83 mm. There was no overlap in the tail lengths of *P. polionotus* and *P. maniculatus*. No single character separated *P. leucopus* from *P. maniculatus*.

Multivariate analyses using external and skull measurements were successful in identifying the four species. Stepwise discriminant analysis correctly classified all specimens using measurements of 13 characters (in order of inclusion into model: Tail, SL, MTL, Foot, RL, OC, PFL, Body, TTL, PB, BNL, PL, PW). The three axes accounted for 55.51, 37.16, and 7.34% of the variance (Fig. 3a). After a varimax rotation, the variables most highly correlated with the first discriminant function were TTL (0.87), SL (0.85), BNL (0.74), PL (0.69), RL (0.58), PFL (0.58), ZB (0.57), MTL (0.53), and NL (0.52); those highly correlated with the second function were BD (0.82), PB (0.40), and OC (0.37); and those highly correlated with the third function were PFL (0.49), RL (0.45), PB (0.23), and OC (-0.21).

Discriminant analysis using only skull measurements correctly classified at most 90% of the specimens with 10 characters (in order of inclusion into model: SL, BD, MTL, RL, PFL, OC, TTL, BNL, PB,

Table 2. Unstandardized discriminant function coefficients using one or two morphological characters of four *Peromyscus* species in the southeastern United States. Each cell contains characters used, coefficients, constants, and numbers of errors for each set of species. Discriminant scores for each pair of species have opposite signs, and this is indicated as one species greater than zero. Cells above the diagonal are skull only; cells below the diagonal are external and skull characters. Variables defined in the Methods.

	<i>P. gossypinus</i>	<i>P. leucopus</i>	<i>P. maniculatus</i>	<i>P. polionotus</i>
<i>P. gossypinus</i>				
	SL	0.927	SL	SL
	MTL	3.732	BD	C
	C	-32.229	C	-39.78
	Pg scores > 0		Pg scores > 0	Pg scores > 0
	Errors: P1 2; Pg2		Errors: none	Errors: none
<i>P. leucopus</i>				
	Foot	0.593	OC	SL
	SL	0.821	BD	MTL
	C	-34.125	C	C
	Pg scores > 0		Pl scores > 0	Pl scores > 0
	Errors: Pg 5; Pl 1		Errors: Pm 15; Pl 24	Errors: Pp 1; Pl 2
<i>P. maniculatus</i>				
	BNL	0.685	Tail	SL
	BD	2.403	BNL	TTL
	C	-37.611	C	C
	Pg scores > 0		Pm scores > 0	Pm scores > 0
	Errors: Pg 1; Pm 0		Errors: Pl 0; Pm 1	Errors: Pp 4; Pm 8
<i>P. polionotus</i>				
	Tail	1	Tail	1
	C	-55	SL	-60
			C	
	Pg scores > 0		Pl scores > 0	Pm scores > 0
	Errors: none		Errors: Pl 3; Pp 0	Errors: none

PW). After a varimax rotation, the variables most highly correlated with the first discriminant function were SL (0.74), TTL (0.74), BNL (0.66), PFL (0.66), RL (0.65), PL (0.62), Foot (0.59), MTL (0.53), ZB (0.53), and NL (0.50); the only variable highly correlated with the second function was Tail (0.82, all others were less than ± 0.17); at -0.33, OC was most highly correlated with the third function. All the misclassifications of the data were in separating *P. leucopus* and *P. maniculatus* (Fig. 3b). This observation led us to implement a two-step discrimination process as suggested by Thompson and Conley (1983). First, we grouped *P. leucopus* and *P. maniculatus* and performed discriminant analysis among *P. gossypinus*, *P. polionotus*, and *P. leucopus*-*P. maniculatus*; then we separated *P. leucopus* and *P. maniculatus*. However, this scheme did not improve the classification results.

In analysis of species pairs, at least 98% of specimens could be separated using only one or two external and/or skull measurements (Table 2). In pairwise comparisons using only skull measurements, we could separate at least 95% of the specimens (except for *P. leucopus*-*P. maniculatus*). For this species pair two characters separate 82% of the specimens. The scores generated by the discriminant functions (Table 2) approximately fall on either side of zero, such that scores for one species are positive, and scores for the other species are negative. However, these models do generate a few misclassifications; therefore, specimens with scores near zero (e.g., ± 0.5) should be subjected to the full discriminant models.

DISCUSSION

Discrimination of these *Peromyscus* species is difficult when collection location information or skins are missing, and we did not achieve the ultimate goal of this project which was to correctly classify any skull without external information. However, the great majority of specimens can be correctly assigned to species, and the discriminant function was useful in identifying likely misclassified and questionable specimens in our museum collections. Additionally, the function allows evaluation of specimens collected at the periphery of species' ranges.

The model using external and skull characters was reasonably successful in classifying the test specimens, which suggests that we captured enough of the variation within each species to make it useful in classifying specimens from somewhat beyond the geographic distribution of our samples. This is an improvement over the ad hoc approach where each state or region requires a different discrimination model. However, although the *P. maniculatus* test specimens classified correctly, they tended to fall in the margins of the discriminant score distributions. The model with only skull measurements was less successful in classifying

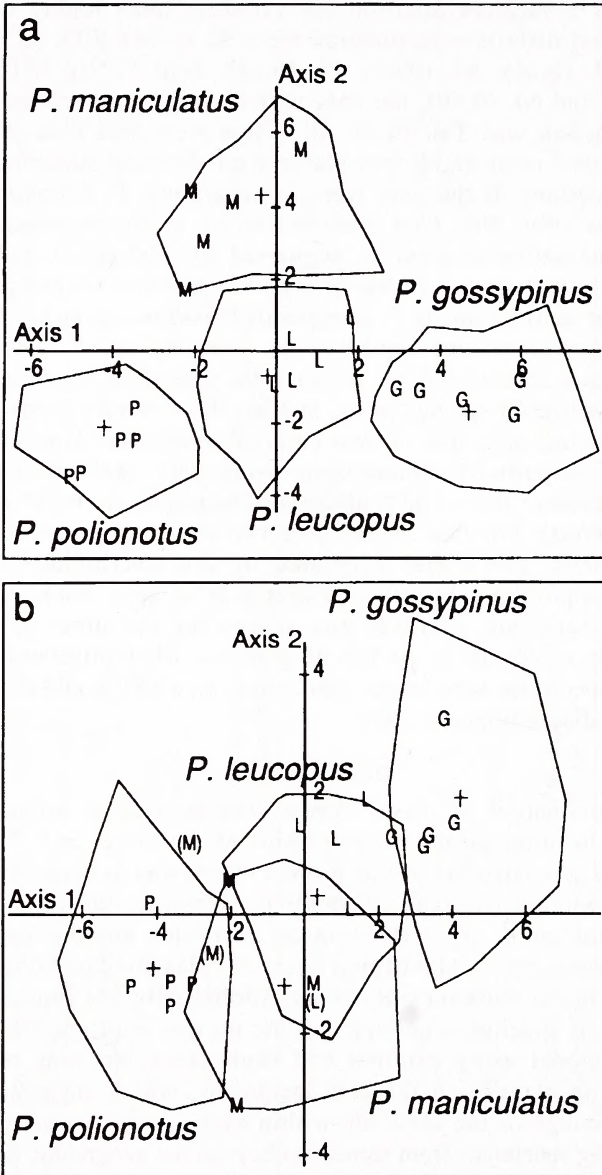


Fig. 3. Distribution of discriminant scores generated from (a) external and skull measurements and from (b) skull measurements alone plotted on the first two canonical axes. Letters (the first letter of the specific epithet for each species) designate the location of test specimens, letters in parentheses mark misclassifications, and crosses mark group centroids.

the test specimens, and results should be viewed with caution if that model is used for specimens collected far outside the geographic distribution of our samples.

Our results were similar to those of previous authors who found that these species tend to differ significantly in most measurements, but that there is generally some overlap in measurement that prevents classification of some specimens based on single characters. For example, Linzey et al. (1976) could separate most specimens using anterior palatal foramen length and width or skull length. Choate (1973) could separate most specimens with tail length. Engstrom et al. (1982) found that *P. gossypinus* differed significantly from *P. leucopus* in every character they measured, but that there was overlap in all characters. McCarley (1954) found that hindfoot length separated most *P. leucopus* from *P. gossypinus*.

Stromberg (1979) successfully used discriminant analysis on external characters to separate *P. maniculatus* from *P. leucopus*. We found that these characters could not be used in the extreme Southeast (Fig. 2). However, he found that ear length was especially useful, and we were not able to include that character. We disagree with Stromberg's (1979) statement that discrimination of external characters offers a dependable alternative to cranial measurements in the identification of *P. maniculatus* and *P. leucopus*. As in our study, McDaniel et al. (1983) and Choate et al. (1979) were able to separate almost all of their specimens using cranial measurements. Only Engstrom et al. (1982) was able to separate all of their specimens using cranial measurements.

Choate (1973), Choate et al. (1978), and Engstrom et al. (1982) found that variation among adult age classes was required in the models for accurate classification. In contrast, we did not find that age variation among adult age classes (4–6, Schmidly 1973) was significant. We found statistical differences among age classes 4–6, but these differences were small relative to the differences among species, and thus age information was not important in our models.

Several authors have found ratios useful in identifying *Peromyscus* species pairs. McDaniel et al. (1983) found that the ratio of interorbital width to length of the nasal bone was useful in separating *P. attwateri* from *P. gossypinus*. Feldhamer et al. (1983) found that the ratio of tail length to body length in conjunction with body mass separated *P. leucopus* from *P. maniculatus* (pregnant females excluded). McCarley (1954) used the ratio of skull length to foot length to identify *P. gossypinus*, *P. leucopus*, and their purported hybrids. Although ratios may provide useful indices, we agree with Humphries et al. (1981) and the references they provide that ratios should be avoided in morphometric

studies because of statistical and conceptual difficulties. Discriminant analysis based on two characters has a similar result of separating groups based on the magnitude of two measurements. It also has the benefits of potentially better separation of groups by stretching the axes (weighing measurements with discrimination function coefficients) and an associated probability of group membership. Therefore, we have presented results (Table 2) that use one or two measurements rather than ratios to separate pairs of species with discriminant functions.

We agree with Choate (1973) that habitat and external features (e.g., tail coloration, penciled tail, color, and degree of fur luxuriance) can yield important information for classifying these species. For example, we believe that the best ways to identify *P. polionotus* are that it is found on sandy soils and by its short, strongly bicolored tail, and the best ways to identify *P. leucopus* are that it is found in low elevation exeric sites and that it has more reddish-orange on the sides than *P. gossypinus*. Other qualitative characters may also be useful. For example, Linzey et al. (1976) found that the skulls of *P. leucopus* tend to be lighter and more fragile than those of *P. gossypinus*. However, our goal was to identify these species with quantitative characters rather than qualitative characters, and preferably with the skull alone, as noted by Feldhamer et al. (1983), these qualitative characteristics can be variable within species. Most of the classification problems we encountered involved old skulls without associated skins.

Use of the discriminant function—Discriminant analysis combines variables to generate a set of linear, independent axes upon which specimens, after appropriate scoring, can be plotted and their classification determined. The appropriate scoring method is to multiply each morphological character variable (e.g., foot length, skull length) by its discriminant function coefficient, sum the products, and add a constant (for each axis separately). In general:

$$D_1 = B_{10} + B_{11}X_1 + B_{12}X_2 + B_{13}X_3 + \dots + B_{1n}X_n$$

$$D_2 = B_{20} + B_{21}X_1 + B_{22}X_2 + B_{23}X_3 + \dots + B_{2n}X_n$$

where D_1 is the specimen's discriminant score on the first axis, the B_{1i} 's are discriminant function coefficients estimated from the data for the first axis (B_{10} 's are constants), and the X_i 's are the values of the original variables. This is done separately for each axis, and the scores, D_1, D_2, \dots, D_n , form the coordinate of the specimen's location in the n -dimensional discriminant space. For example, to separate *P. gossypinus* from *P. leucopus* using external and skull measurements, the appropriate transformation is (only one axis is needed)

$$D = -34.125 + 0.593(\text{hindfoot length}) + 0.821(\text{skull length}).$$

Table 3. Unstandardized canonical discriminant function coefficients, external and skull characters, and skull characters only for four *Peromyscus* species in the southeastern United States.

Character	External and Skull			Skull Only		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Body	-0.009	-0.03	0.013			
Foot	0.366	-0.016	-0.008			
Tail	-0.002	0.194	0.005			
SL	0.633	-0.199	-1.295	1.13	-0.602	-0.944
BNL	-0.287	-0.38	-0.325	-0.465	0.782	-0.419
RL	0.443	0.043	2.687	-0.356	0.121	2.714
OC	0.511	-0.482	-1.636	0.393	1.055	-1.326
PL	-0.338	-0.151	0.058			
MTL	2.041	-0.461	0.434	2.016	0.31	1.219
TTL	0.567	0.355	-1.174	1.342	-1.551	-0.908
PW	-0.007	-0.764	0.995	-0.31	0.762	1.107
PB	1.11	-0.583	1.458	-0.365	2.57	1.766
BD				-0.074	2.958	-0.047
PBL	0.997	-0.298	2.225	0.298	-0.233	2.514
Constant	-37.36	8.115	20.128	-38.27	-21.09	6.454

Table 4. Group centroids for external and skull characters and for skull characters only based on unstandardized canonical discriminant function coefficients of four *Peromyscus* species in the southeastern United States.

Species	External and Skull Characters			Skull Characters Only		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
<i>P. gossypinus</i>	4.710	-1.654	-0.811	4.309	1.915	0.817
<i>P. leucopus</i>	-0.099	-0.671	-1.337	0.356	0.308	-1.261
<i>P. maniculatus</i>	-0.354	4.328	0.491	-0.528	-1.196	0.164
<i>P. polionotus</i>	-4.209	-2.108	1.616	-4.121	-1.000	0.255

Given an unknown specimen with hindfoot and skull lengths of 23.5 and 28.7 mm, respectively, and the coefficients of these measurements from Table 3, this equation becomes:

$$D = -34.125 + 0.593(23.5) + 0.821(28.7)$$

$$D = 3.377$$

In this case, any positive value of D indicates *P. gossypinus*, and any negative value of D indicates a *P. leucopus* (Table 2). Thus, this specimen is a *P. gossypinus*.

If these two species required more than one axis, D_1 and D_2 would be calculated using discriminant coefficients from Table 3 for external and cranial measurements or Table 4 for skull measurements only. The bivariate coordinate (D_1, D_2) can be plotted on a 2-dimensional graph (e.g., Fig. 3).

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APPENDIX

Specimens examined to build the model.

Museum acronyms are defined in the acknowledgments. Location names are states and counties.

P. gossypinus—ALABAMA: Jackson; 9 USNM). Tuscaloosa; 7 (UAL). FLORIDA: Alachua; 13 (UF). GEORGIA: Burke; 12 (MCZ), 2 (USNM). Camden; 13 (UGAMNH). Charlton; 22 (UGAMNH). Ware; 8 (UGAMNH). NORTH CAROLINA: Gates; 8 (LSUMZ). SOUTH CAROLINA: Charleston; 16 (CMNH).

P. leucopus—ALABAMA: Colbert; 1 (USNM). Jackson; 4 (USNM). GEORGIA: Barrow; 1 (UGAMNH). Clarke; 40 (UGAMNH). Dekalb; 1 (UGAMNH). Elbert; 1 (UGAMNH). Oconee; 1 (UGAMNH). Rockdale; 1 (UGAMNH). Walton; 1 (UGAMNH). Wilkes; 1 (UGAMNH). NORTH CAROLINA: Anson; 3 (USNM). Jackson; 8 (USNM). Macon; 2 (UGAMNH). Wake; 7 (USNM). SOUTH CAROLINA: Abbeville; 1 (USNM). Greenville; 2 (USNM). Oconee; 7 (USNM). Pickens; 4 (USNM).

P. maniculatus—GEORGIA: Rabun; 9 (UGAMNH). Towns; 9 (UGAMNH). Union; 27 (UGAMNH). KENTUCKY: Bell; 7 (USNM). Harlan; 12 (USNM). NORTH CAROLINA: Macon; 21 (UGAMNH). TENNESSEE: Carter; 9 (USNM). Johnson; 2 (USNM). Sevier; 16 (USNM).

P. polionotus—ALABAMA: Autauga; 7 (USNM). Henry; 7 USNM). Marshall; 1 (USNM). FLORIDA: Indian River; 5 (UGAMNH). Marion; 5 (UGAMNH). GEORGIA: Baker; 2 (UGAMNH). Barrow; 2 (UGAMNH). Burke; 1 (UGAMNH). Clarke; 10 (UGAMNH). Decatur; 3 (UF). Dougherty; 2 (USNM). Gordon; 3 (USNM). Haralson; 3 (UGAMNH). Irwin; 2 (UF). Johnson; 2 (UGAMNH). Lowndes; 2 (UGAMNH). Marion; 1 (UF). McIntosh; 3 (UGAMNH). Randolph; 10 (UGAMNH). Richmond; 2 (UGAMNH). Seminole; 2 (UF). Taylor; 1 (USNM). Tift; 13 (USNM). SOUTH CAROLINA: Aiken; 12 (UGAMNH). Barnwell; 9 (UGAMNH).

Specimens examined to test the model.

P. gossypinus—ALABAMA: Dekalb; 2 (UI). GEORGIA: Dougherty; 2 (UI). SOUTH CAROLINA: Aiken; 1 (UGAMNH).

P. leucopus—KENTUCKY: Bell; 1 (UGAMNH). NORTH CAROLINA: Gates; 2 (UGAMNH). McDowell; 2 (UGAMNH).

P. maniculatus—GEORGIA: Fannin; 2 (UGAMNH). NORTH CAROLINA: Watauga; 1 (USNM). TENNESSEE: Carter; 1 (UGAMNH). VIRGINIA: Giles; 1 (UGAMNH).

P. polionotus—ALABAMA: Marshall; 1 (USNM). FLORIDA: Highlands; 2 (UGAMNH). Marion; 1 (UGAMNH). SOUTH CAROLINA: Barnwell; 1 (UGAMNH).

Small Mammal Communities in Streamside Management Zones

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ABSTRACT—Populations of small mammals were sampled in six streamside management zones (SMZs) of three widths: narrow (15 m), medium (30 m), and wide (50 m), which extended through a three-year-old pine plantation. We also sampled the pine plantation and a nearby mature riparian forest. Two hundred and twenty-eight small mammals from 12 species were captured in 8,640 trapnights. Overall, capture rates were not related to SMZ width. During summer, capture rates were greater in the mature riparian forest than in SMZs. Abundance of individual species varied among the habitats sampled. SMZs supported populations of *Oryzomys palustris*, *Ochrotomys nuttalli*, and *Neotoma floridana*, three species not found in the pine plantation. Inclusion of SMZs in pine plantation management can enhance habitat diversity and contribute to local diversity of the small mammal community.

Approximately 8.5 million hectares in the southern United States is maintained in pine plantations (United States Department of Agriculture, Forest Service 1988), much of which is managed on short rotations. Although young pine plantations provide seasonal habitat needs for several mammalian species including white-tailed deer (*Odocoileus virginianus*), eastern cottontails (*Sylvilagus floridanus*), and oldfield mice (*Peromyscus polionotus*), other later-successional species may be low in abundance or absent.

Streamside management zones are designed to protect water quality from potential impacts of silvicultural operations. SMZs also add habitat diversity to the surrounding pine plantations. Additionally, SMZs create an area of edge, which increases the number of niches available to wildlife.

Squirrel (*Sciurus* spp.) use of SMZs is greater than in adjacent upland pine-hardwood areas in Mississippi (Warren and Hurst 1980) and Alabama (Fischer and Holler 1991), and greater than in adjacent pine plantations in Texas (McElfresh et al. 1980). Studies in eastern Texas indicated that squirrels were more abundant in wide SMZs (>55 m) than in narrow SMZs (<25 m). Conversely, small mammals were more abundant in the narrow SMZs (Dickson and Huntley 1987,

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Dickson and Williamson 1988). Nevertheless, the relationships between SMZ width and small mammal communities have not been investigated adequately. We censused the small mammal communities in SMZs of varying width, in adjacent pine plantations, and in mature riparian areas.

MATERIALS AND METHODS

Study areas were located in the Upper Coastal Plain of Georgia on the Ogeechee River drainage in Jefferson and Emanuel counties. All SMZs were along first order streams in a 450-ha pine plantation owned by Federal Paper Board Company. The stand was clearcut in 1985, the site prepared chemically, and planted in a 2-m X 3-m spacing to loblolly pine (*Pinus taeda*) in 1987. All SMZs were selectively harvested. Remaining overstory in the SMZs was dominated by blackgum (*Nyssa sylvatica*), tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), and loblolly pine. Understory composition in the SMZs was dominated by blackberry (*Rubus* spp.), greenbriar (*Smilax* spp.), poison ivy (*Toxicodendron radicans*), gallberry (*Ilex glabra*), and fetterbush (*Lyonia lucida*).

Three width categories of SMZs were compared using two replicates of each: narrow (15–18 m), medium (28–30 m), and wide (49–53 m). Additional plots were established along two creeks in mature, riparian forests on Old Town Plantation near Louisville, Georgia. Streams in these forests averaged 2 m in width and were at least 100 m away from any forest edge. Dominant overstory included loblolly pine, cypress (*Taxodium distichum*), hickory (*Carya* spp.), oaks (*Quercus* spp.), sweetgum, and red maple.

Populations of small mammals were sampled by removal trapping along a 200-m transect in the center of each SMZ and along the stream in the mature riparian area. An additional transect was established just inside the outer edges of the medium and wide SMZs. Parallel 200-m transects were sampled in the adjoining pine plantations, 50 m from the SMZ edge. Transect paths were lightly cleared for access. Ten trapping stations were placed at 20-m intervals along each transect.

Small mammal populations were censused during four consecutive nights in December 1990, June 1991, January 1992, and June 1992. Sampling did not occur on rainy days. One Victor™ mouse trap, a Victor™ rat trap, and a pitfall trap were placed at each trapping station. Snap traps were baited with a mixture of peanut butter and peanut oil. Pitfall traps (10-cm diameter, and filled to a depth of 7 cm with water) were used to increase trapping success for shrews. Shrews

are difficult to catch with conventional snap or live traps (Szaro et al. 1988, Rose et al. 1989). Captured animals were donated to The University of Georgia Museum of Natural History.

Captures were combined by season over the 2-year trapping period and treated as replicates. Differences in mean capture rates were tested by analysis of variance, and Duncan's Multiple Range Test was used to separate means ($\alpha=0.05$).

RESULTS AND DISCUSSION

We captured 228 small mammals from 12 species in 8,640 trapnights. Southern short-tailed shrews (*Blarina carolinensis*) accounted for 24.5% of all captures. White-footed (*Peromyscus leucopus*) and cotton mice (*P. gossypinus*) were grouped together as cotton mice, because of the difficulty in positive identification. Morphological criteria used to separate the species are of limited value when applied to subadult mice (Dickson and Williamson 1988). Cotton mice accounted for 20.2% of the animals caught, followed by cotton rats (*Sigmodon hispidus*, 17.1%), old-field mice (*Peromyscus polionotus*, 13.6%), least shrews (*Cryptotis parva*, 11.0%), rice rats (*Oryzomys palustris*, 7%), and golden mice (*Ochrotomys nuttalli*, 3.1%). Other species captured included the woodrat (*Neotoma floridana*), Eastern harvest mouse (*Reithrodontomys humulis*), Southeastern shrew (*Sorex longirostris*), pine vole (*Microtus pinetorum*), and Eastern mole (*Scalopus aquaticus*).

During winter sampling periods, small mammal capture rates did not vary by treatment ($P = 0.56$). However, in summer total capture rates were greater in the mature riparian forest than in the other habitats sampled. Several species showed significant habitat preferences (Table 1). During both winter and summer, cotton mice were trapped more frequently in the mature riparian forest than in the other habitats sampled. The preferred habitat for the cotton mouse is bottomland hardwood forest subject to frequent flooding (Cothran et al. 1991). Cotton mice were equally abundant in SMZs and pine plantations.

In winter, oldfield mice were most common on the pine transects. Several studies have reported the preference of oldfield mice for early successional habitats (Golley et al. 1965, Brooks 1992). Oldfield mice, harvest mice, and cotton rats prefer areas with stands of dense grass. Cotton rats were caught most frequently in narrow SMZs in winter, and no habitat preference was observed in summer. The rice rat was not recorded in the pine plantations in either season. Southern short-tailed shrews, which prefer moist habitats (Szaro et al. 1988), occurred

Table 1. Small mammal capture rates ($\bar{x} \pm \text{SE}$) per trapline by species, season, and treatment over two years of trapping near Louisville, Georgia.¹

Season	Treatment	n ²	Cotton Mouse	Oldfield Mouse	Cotton Rat	Rice Rat	Southern Shrew	Short-tailed Shrew	Golden Mouse
Winter									
3-yr-old plantation	Narrow SMZs	12	0.08±0.08B	1.92±0.51A	0.42±0.33B	0	0.25±0.13AB	0	0
	Medium SMZs	4	0.50±0.50B	0.50±0.29B	3.50±1.50A	0.50±0.50	0	0	0
	Wide SMZs	8	0.50±0.27B	0.25±0.25B	0.38±0.18B	0.62±0.32	0.50±0.27AB	0	0
	Mature Riparian Forest	4	0.25±0.16B	0.13±0.13B	0.50±0.27B	0.38±0.38	1.38±0.59A	0.38±0.38	0
Summer	3-yr-old plantation	12	3.75±1.65A	0	0	0	0.50±0.50AB	0.25±0.25	0
	Narrow SMZs	4	0.75±0.18B	0.25±0.12	0.50±0.15	0	0.67±0.22	0	0
	Medium SMZs	8	0.25±0.25B	0	0.50±0.50	0	0.50±0.29	0	0
	Wide SMZs	8	0	0	0.50±0.27	0.38±0.18	0.88±0.23	0	0
Mature Riparian Forest	3-yr-old plantation	12	0.13±0.13B	0	0.13±0.13	0.25±0.16	1.50±0.42	0	0
	Medium SMZs	4	2.75±1.80A	0	0	0.25±0.25	1.50±0.29	0	0
	Wide SMZs	8	0	0	0	0	0	0	0
	Mature Riparian Forest	4	0	0	0	0	0	0	0
Spring									
Summer									
3-yr-old plantation	Narrow SMZs	12	0	1.25±0.41	0	0.08±0.08	0.16±0.11	0.08±0.08	0
	Medium SMZs	4	0	0	0.25±0.25	0	0	0	0
	Wide SMZs	8	0	0	0	0	0	0	0
	Mature Riparian Forest	4	0.13±0.13	0.50±0.50	0	0	0	0	0
Summer	3-yr-old plantation	12	0	0.25±0.12	0	0	0	0	0
	Narrow SMZs	4	0	0.50±0.50	0	0	0	0	0
	Medium SMZs	8	0	0	0	0	0	0	0
	Wide SMZs	8	0	0	0	0	0	0	0
Mature Riparian Forest	3-yr-old plantation	12	0.25±0.25	0.25±0.25	0	0	0	0	0
	Medium SMZs	4	0	0	0	0	0	0	0
	Wide SMZs	8	0	0	0	0	0	0	0
	Mature Riparian Forest	4	0	0	0	0	0	0	0

¹Means followed by the same letter or a blank, within the same season and column, are not significantly different at $P = 0.05$ (Duncan's Multiple Range Test).²Number of traplines per treatment.

in all habitats, although they tended to be caught most frequently in the mature riparian forest.

In summer, mature riparian areas were dominated by the cotton mouse, and, along with wide SMZs, were the only areas in which golden mice and woodrats were found. These species often prefer mature hardwood forest habitat, where they eat insects, twigs, green leaves, berries, seeds, and nuts (Cothran et al. 1991). The wide SMZs in our study provided some habitat for species associated with mature stands, such as the golden mouse and the woodrat.

Our results suggest that the species composition of the small-mammal community was affected by SMZ width. Only wide SMZs (49–53 m) maintained populations of small mammal species that are characteristic of mature riparian forests. Rice rats, golden mice, and woodrats were captured in the SMZs, but not in the adjacent pine plantations. Inclusion of SMZs in pine plantation management can enhance habitat diversity and thereby contribute to local diversity of the small mammal community.

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Home Range and Activity Patterns by Gray Foxes, *Urocyon cinereoargenteus* (Carnivora: Canidae), in East Tennessee

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ABSTRACT—We determined home-range size, spatial distribution, and activity patterns of gray foxes (*Urocyon cinereoargenteus*) ($N = 10$) between September 1986 and August 1987 in east Tennessee. Average annual home-range size was 3.97 ± 1.51 ($\bar{x} \pm \text{SE}$) km^2 . There were no significant differences in home-range size between sexes (females 3.67 ± 1.54 ; males 4.27 ± 1.59 km^2) or age groups (adults 4.41 ± 1.46 ; subadults 3.20 ± 1.62 km^2). Home-range sizes were similar in three reproductive seasons and in seasons of predominantly fruit (presumably abundant) and predominantly flesh (presumably more scarce) diets. Home ranges of adult male–female pairs and subadults coincided, suggesting monogamy and exclusive area utilization by family groups. We observed lower sunrise and/or daylight activity levels during breeding and flesh diet seasons, and in months of low foliar cover.

The relationship of body size, metabolic needs, and dietary trophic level to home-range size is well known. Relative to body size, flesh-eaters have larger home ranges than plant-eaters, presumably due to decreasing food base with ascending trophic level (McNab 1963). However, most studies relating home-range size to trophic level are based on interspecific comparisons.

Intraspecifically, seasonal shifts in home-range size appear to be negatively correlated to food availability (Nicholson 1982). Sex, age, and reproductive cycle (MacDonald 1980), population density (Trapp and Hallberg 1975), inter- or intraspecific competition, and habitat quality and dispersion (MacDonald 1980) are also thought to play a role in affecting home-range size.

Most studies indicate that gray foxes are nocturnally active (Yearsley and Samuel 1980, Nicholson 1982, Haroldson and Fritzell 1984). However,

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the amount of time required for foraging and temporal activity patterns might be expected to change in relation to seasonal food availability and/or type.

We obtained concurrent data on food habits, home range, and activity patterns for gray foxes (Greenberg et al. 1988), which provided an opportunity to compare seasonal shifts in dietary trophic level with changes in home-range size. We predicted that home-range size would become smaller as fruit became seasonally available (spring–fall) and would expand in response to a presumably scarcer (predominantly flesh) winter food supply. We also compared reproductive seasons, sex, and age with home-range size.

METHODS

Study Area—The study area was located within the National Environmental Research Park on the Department of Energy's Oak Ridge Reservation, approximately 28 km west of Knoxville, Tennessee (35°58' N, 84°56' W). Vegetation community types included pine and pine-hardwood forests, loblolly pine (*Pinus taeda*) plantations, eastern red cedar (*Juniperus virginiana*) barrens, oak-hickory forests, bottomland hardwood forests, old fields, and developed areas. The Tennessee Valley Authority's Melton Hill Reservoir and Watts Bar Lake border the reservation on the west, south, and east; streams and springs throughout the area provided water and wetland habitat.

The geology of the reservation is characteristic of the Southern Appalachian Valley and Ridge Province. Parallel, southwest–northeast-oriented ridges separated by valleys (elevation ranged from 226 to 413 m) lend additional diversity to the landscape.

Radio Telemetry—Foxes were captured in Number 1.5 Victor soft-catch leg-hold traps with dirt-hole sets and drags. Attractants included fox urine, fox gland lures, pork cracklings, fish oil, and muskrat oil. Foxes were anesthetized with 5–10 mg/kg ketamine hydrochloride (Ketaset) or not anesthetized (Nicholson 1982). Animals were eartagged, fitted with radio collars equipped with a mercury tip-switch activity sensor (Telonics, Mesa, Arizona) in the 150–151.84 frequency range, and released at the trap site. We classified foxes as subadults (<1-year-old) or adults based on tooth wear (Geir 1968).

There were 138 receiving stations established. Animals were located with a four-element, hand-held, Yagi antenna and a portable receiver. Locations and activities were recorded at 2-hour intervals between the hours of 1600 and 0800 weekly. Occasional locations were also recorded between 0800 and 1600. We used ≥ 2 compass

bearings with an intersecting angle $\geq 45^\circ$ and $\leq 135^\circ$, and as close to 90° as possible (Heezen and Tester 1967) to plot locations. Activity was recorded. Azimuths were converted to x:y coordinates by the computer program Convxpoly (Boyle 1986), and the data were hand-plotted on a 1:24,000 United States Geological Survey topographic map with the Universal Transverse Mercator grid system.

We estimated home-range sizes by the minimum convex polygon method (Mohr 1947). Atypical peripheral locations (known excursions) were excluded based on subjective knowledge of typical home-range use by the authors (Ables 1968).


Smith et al. (1981) found that three half-night radio-tracking periods provided a larger estimate of coyote home ranges than 30 independent daily locations, and that three or four nights provided good home-range estimates for coyotes with small home ranges. We assumed that their findings also applied to gray foxes. Hence, we considered ≥ 25 locations and at least three track-nights to be an adequate sample size for home-range determinations.


Home ranges were calculated for three reproductive and two dietary seasons. Three reproductive seasons included breeding (January–March), pup-rearing (April–June), and nonbreeding (July–December) (Sullivan 1956, Nowak and Paradiso 1983). Dietary seasons included a dominantly flesh diet (January–April) and dominantly insect or fruit diet (May–December) (Greenberg and Pelton 1991). We compared annual and seasonal home-range sizes between sexes and age groups. Due to small sample sizes and high variance, we used descriptive statistics rather than statistical tests in drawing our conclusions.

We calculated the percentage of “active” locations within four time periods: two at sunrise (0.5 hours prior, 0.5 hours after sunset) and two at night (0.5 hours after sunset, 0.5 hours prior to sunrise). Data were pooled for all animals. We used Chi-square tests to detect temporal differences in activity level, differences among reproductive and dietary seasons, and differences between seasons of low (November–April) and high (May–October) foliar cover.

RESULTS

We obtained 2,247 locations on 12 foxes captured between September 1986 and August 1987 (Fig. 1 and 2). Five adult males, two adult females, and five subadult females were captured. Only 10 animals were included in home-range estimates. Because of variable tracking periods among foxes, some animals could not be used in home-range estimates of reproductive or dietary seasons (Table 1).

 ADULT FEMALE
(74,80)

 SUBADULT FEMALE
(62,63,64,66,72)

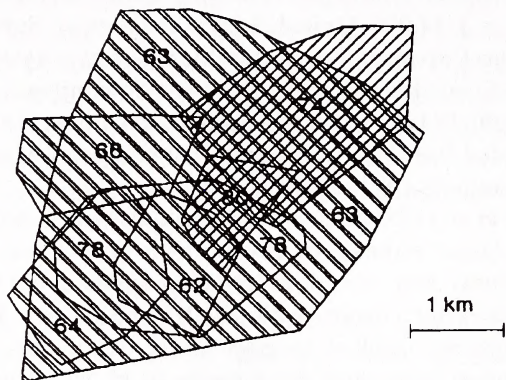



Fig. 1. Composite home ranges of two adult and five subadult female gray foxes on the Oak Ridge Reservation in east Tennessee, September 1986–August 1987.

 ADULT MALE (58, 69, 76, 82, 84)

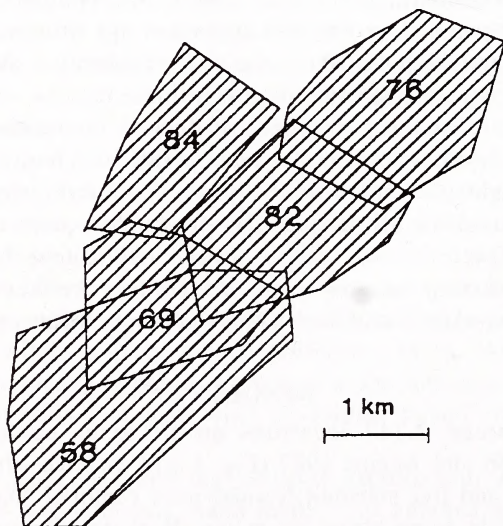


Fig. 2. Composite home ranges of five adult male gray foxes on the Oak Ridge Reservation in east Tennessee, September 1986–August 1987.

Table 1. Annual minimum cover polygon home-range estimates (km²) for five male and seven female gray foxes radiotracked from September 1986 to August 1987, Oak Ridge Reservation in east Tennessee.

ID	Sex	Age	Number of Locations	Tracking Period	Annual Home-Range Size (km ²)
58	M	Adult	25	03/16/87–08/31/87	6.91
69	M	Adult	231	09/25/86–06/09/87	3.25
76	M	Adult	248	09/14/86–08/31/87	4.36
82	M	Adult	293	09/07/86–08/31/87	4.01
84	M	Adult	130	09/11/86–03/02/87	2.83
62	F	Subadult	102	10/01/86–01/12/87	2.09
63	F	Subadult	119	02/25/87–08/31/87	17.94 ^{1,2,3}
64	F	Subadult	236	09/26/86–05/12/87	3.08
66	F	Subadult	271	09/25/86–08/31/87	2.09
74	F	Adult	266	09/14/86–08/31/87	5.08
78	F	Subadult	308	09/19/86–08/31/87	5.54
80	F	Adult	18	09/09/86–11/03/86	1.24 ^{1,2,3}

¹ Omitted from reproductive season home-range analysis; insufficient data.

² Omitted from dietary season home-range analysis; insufficient data.

³ Omitted from annual home-range analysis; insufficient data.

Mean annual home-range size ($\bar{x} \pm \text{SE}$) for 10 gray foxes was $3.97 \pm 1.51 \text{ km}^2$. Home-range size was similar between males ($N = 5$; $4.27 \pm 1.59 \text{ km}^2$) and females ($N = 5$; $3.67 \pm 1.54 \text{ km}^2$), and between adult ($N = 6$; $4.41 \pm 1.46 \text{ km}^2$) and subadult ($N = 4$; $3.20 \pm 1.62 \text{ km}^2$) foxes.

Home-range size was similar during fruit diet ($N = 9$; 2.92 ± 0.40) and flesh diet seasons ($N = 9$; 3.43 ± 0.48). Home-range sizes were similar among reproductive seasons for all foxes ($N = 8$; 2.72 ± 0.17); ($N = 7$; 2.32 ± 0.43); and ($N = 9$; 2.83 ± 0.42) for breeding, pup-rearing, and pre-breeding seasons, respectively. Within reproductive seasons, male and female home-range sizes also were similar ($N = 4$; 2.67 ± 0.11) versus ($N = 4$; 2.7 ± 0.30) for breeding; ($N = 3$; 2.79 ± 0.59) versus ($N = 4$; 1.98 ± 0.55) for pup-rearing; and ($N = 4$; 2.60 ± 0.30) versus ($N = 5$; 3.01 ± 0.67) for pre-breeding seasons, respectively. We observed that whelping females exhibited restricted movements during pup-rearing season.

Adjacent home ranges of four adult males were nearly exclusive except for excursions by M 69 and M 76 into M 82's home range during breeding season (Fig. 2). Subadults F 64, F 62, and F 78 home ranges were contained within adult M 69's home range; F 64 and

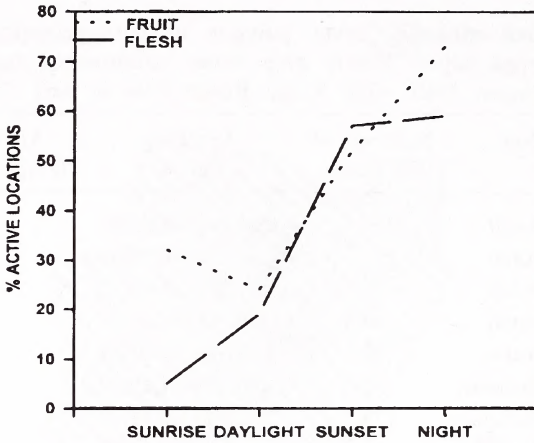


Fig. 3. Diet-related (fruit versus flesh) activity levels (%) of gray foxes radiotracked on the Oak Ridge Reservation in east Tennessee, September 1986–August 1987.

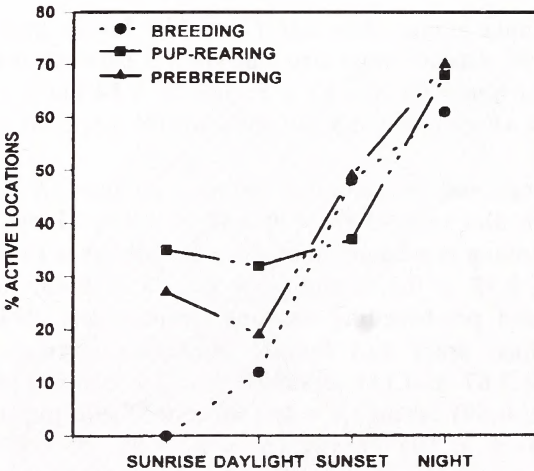


Fig. 4. Reproduction-related activity levels (%) of gray foxes radiotracked on the Oak Ridge Reservation in east Tennessee, September 1986–August 1987.

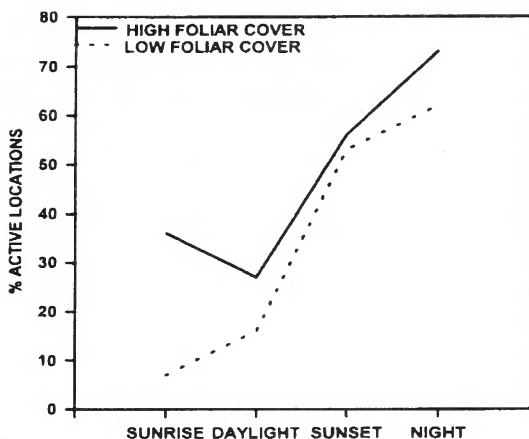


Fig. 5. Cover-related activity levels (%) of gray foxes radiotracked on the Oak Ridge Reservation, east Tennessee, September 1986–August 1987.

F 62 alternately used the same resting places. Adult male–female pairs sharing home ranges include M 82 with F 80 (who died before an adequate sample size was obtained for inclusion in home-range analysis) and M 76 with F 74. Adult same-sex fox home ranges overlapped little, whereas adult male–female pairs and adult–subadult home ranges overlapped substantially. Subadult F 63 had an aberrantly large “home range,” which may have been explorations instead of a home range at all.

Gray foxes were active on a greater proportion of locations in evening and night hours than during sunrise and daylight hours. Animals exhibited a lower sunrise activity level during flesh diet than fruit diet season ($\chi^2 = 17.8$, $P < 0.0005$) (Fig. 3). Lower sunrise activity levels were observed during breeding season, and higher daylight activity was observed during pup-rearing season than during other reproductive seasons ($\chi^2 = 29.8$, $P < 0.0005$) (Fig. 4). Lower sunrise and daylight activity levels were observed during months of low foliar cover than during months of high cover ($\chi^2 = 32.3$, $P < 0.0005$) (Fig. 5).

DISCUSSION

Gray fox home-range sizes were within the range of those reported in other studies (Richards and Hine 1953, Fuller 1978, Yearsley and Samuel 1980, Nicholson 1982, Hallberg and Trapp 1984, Haroldson and Fritzell 1984, Wooding 1984). Nearly exclusive home

ranges shared by adult male-female pairs and subadults suggested that family units are spatially segregated. However, this conclusion is tentative because uncollared foxes may have lived undetected within the study area. Trapp and Hallberg (1975) suggest that a family shares a home range exclusive of others, and they provide some evidence for territoriality.

We were unable to detect any influence of seasonal dietary composition or dietary trophic level on home-range size. Instead, we suggest that diverse, interspersed habitat types within home ranges might provide sufficient food supply in all seasons. Maintaining a home range encompassing sufficient habitat area and types to provide a year-round food supply might be a better strategy than shifting home-range size in response to fluctuating patch productivity or food availability (MacDonald 1980). Further study, including a larger sample size, is warranted to determine the influence of seasonal diet on gray fox home-range size.

Trends in home-range size indicate that males may range farther than females during breeding season. High variance and small sample size may obscure detection of seasonal differences in patterns of home-range size or differences among age groups or sexes.

Predominantly nocturnal activity has been reported in other studies (Nicholson 1982). Lower levels of sunrise activity during flesh diet season, breeding season, and months of low foliar cover could all be a response to sparse cover (November-April). Energy conservation during a period of lower food availability may be a factor. Higher daylight activity during pup-rearing season than during other seasons might be due to increased energy requirements for both parents and pups.

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External Morphometrics of Black Bears, *Ursus americanus*
(Carnivora: Ursidae), in the Great Dismal Swamp
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ABSTRACT— We report body measurements of black bears (*Ursus americanus*) for Great Dismal Swamp, a seasonally-flooded, forested wetland in the Atlantic Coastal Plain. For most body measurements, males reached adult size by 5 years of age and females by 3–4 years of age. Chest girth, and zygomatic circumference were the best ($P < 0.001$) predictors of body mass for both sexes. External morphometrics can be used to predict nutritional condition. Growth models using mass or length data can be developed and growth rates compared among populations. Such comparisons may shed light on black bear taxonomy or habitat quality.

Published data on black bear external morphometrics, other than body mass, are scanty, although common in unpublished theses. Sauer (1975) reported a large data set of external measurements of black bears from New York. Other publications containing data on black bear morphometrics include Poelker and Hartwell (1973:89–104), Cherry and Pelton (1976), and Juniper (1978) from Washington, Tennessee, and Quebec, respectively.

Body morphometrics and growth are important characters in the study of intraspecific regional variation. In a mammal with a wide distribution such as the black bear, such data may provide insights into relationships among environmental factors, particularly nutrition, and genetic potential. For example, mean body masses of adult (≥ 5 -year-old) male black bears range from 96 kg in western Montana (Jonkel and Cowan 1971) to 183 kg in Pennsylvania (Alt 1980), a range mirrored by differences in reproductive rates and attributed to differences in food availability (Bunnell and Tait 1981). Kingsley et al. (1988) found differences in growth curves and body size in three

disjunct populations of brown bears (*Ursus arctos*). They attributed variation to differences in system productivity or bear density.

As part of a larger project studying black bear ecology and physiology in Great Dismal Swamp, we collected body measurements from live-captured black bears (*Ursus americanus americanus*) (Hall 1981). Our objectives were to provide baseline data on body measurements by age for black bears in the Atlantic Coastal Plain and to produce prediction equations for body mass based on morphometric measurements.

MATERIALS AND METHODS

We conducted research from April 1984 to August 1986 on a 555-km² study area containing the 440-km² Great Dismal Swamp National Wildlife Refuge, 57.5-km² Dismal Swamp State Park, and adjacent private land. Descriptions of the study area were reported elsewhere (Hellgren and Vaughan 1988, 1989a). We captured 101 different bears 120 times with spring-activated cable snares during April through December. Bears were immobilized with a 2:1 mixture of ketamine hydrochloride and xylazine hydrochloride at a concentration of 300 mg/mL administered intramuscularly at an initial dosage rate of 6.6 mg/kg. Mass was measured to the nearest kg with a hanging spring scale.

We took measurements on immobilized animals to the nearest mm. Body length was measured from the tip of the snout to the distal end of the last caudal vertebra while the animal was in lateral recumbency. Head length was measured from the tip of the nose to the occiput. Neck girth was measured in the middle of the neck. Chest girth was measured immediately posterior to the scapulae. Circumferences of wrist and elbow (at olecranon process) also were measured. Zygomatic circumference was measured anterior to the ears. The above measurements were taken with a cloth tape pulled snug. Tail length (from base of tail to distal end of caudal vertebra), ear length (from inner notch to tip of pinna), forepaw and hindpaw width (greatest distance across pads), and forepaw and hindpaw length (longest distance along length of pads) were measured with a steel tape. Canine measurements were taken with dial calipers to the nearest 0.1 mm. Upper and lower canine breadths were the distance between the tips of the right and left maxillary and mandibular canines, respectively. Upper and lower canine lengths were measured from the gum line to the tip of the canine. Anterior-posterior lengths and lingual-labial widths of upper and lower canines were measured at the gum line.

We used one-way analysis of variance to examine age differences in physical characteristics within each sex. We did not analyze data

for differences by sex because of obvious size dimorphism. Because of small sample sizes and asymptotic growth, all animals ≥ 7 years old were placed into one age category. Samples were pooled across seasons, and all data were analyzed. When data collected after 15 September ($n = 19$) were deleted, mean body mass for males and females decreased by a maximum of 2.1 and 6.0 kg for any year class. Previous analyses showed an age-season (age categorized as adults or subadults) interaction ($P = 0.06$) in body mass for females and non-significant seasonal variation ($P = 0.11$) for males (Hellgren and Vaughan 1989b), probably because of small samples in fall and, subsequently, weak statistical power. We used Tukey's studentized range test to separate means. Recapture data for individuals recaptured within the same year were not included in any analyses. Recaptures in different years ($n =$ seven male, nine female) were treated as independent observations. Simple linear regression was used to develop relationships among body mass and body measurements.

RESULTS AND DISCUSSION

Ages ranged from 1 to 16 years for males ($n = 71$). All morphometric variables measured varied ($P < 0.001$) by age except ear length ($\bar{x} \pm \text{SE}$) (119 ± 1 mm, $n = 64$) and tail length (73 ± 2 mm, $n = 65$) (Table 1). Based on means separation, we concluded that adult size was reached for most body and canine measurements by 5 years of age. Body mass continued to increase until 6 years of age, with a maximum mass of 198 kg for a 7-year-old individual captured in July.

It is interesting to note the lack of morphometric differences ($P > 0.05$) between 3- and 4-year-old male bears. The stress of competing for access to reproducing females may reduce body growth in these young males, as nutrients are partitioned away from growth and into demands for mate-searching and male-male aggression (Garshelis and Hellgren 1994).

Females ranged in age from 1 to 9 years ($n = 37$). Body measurements that did not vary by age ($n = 34$) were ear length (112 ± 1 mm), tail length (74 ± 3 mm), forepaw width (83 ± 1 mm), forepaw length (85 ± 1 mm), hindpaw length (79 ± 1 mm), and hindpaw length (147 ± 1 mm). Female adult size was reached at an earlier age than male adult size (Table 2). Adult size in body measurements was generally reached by 3 or 4 years, whereas adult canine size was reached by 2 years of age. In New York, female bears attained adult size for all measured characteristics by 2.5 years (Sauer 1975).

Morphometric data are limited for other southeastern wetland bear populations. Adult (>3 years) males and females weighed an

Table 1. Morphometric characteristics (mm unless otherwise noted) of male black bears significantly affected ($P < 0.001$) by age in Great Dismal Swamp.

Characteristics	Age (years)																				
	1 (<i>n</i> =3-5)		2 (<i>n</i> =9-14)		3 (<i>n</i> =11-14)		4 (<i>n</i> =8-13)		5 (<i>n</i> =9)		6 (<i>n</i> =3-6)		7+ (<i>n</i> =8-10)								
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE							
Mass (kg)	46.4	7.7	d ¹		82.0	6.0	c	83.9	4.3	c	114.6	9.9	b	127.3	5.3	ab	148.1	8.0	a		
Total Length	1,227	119	e	1,553	56	d	1,673	30	cd	1,694	38	bcd	1,829	28	abc	1,896	29	ab	1,881	34	a
Head Length	278	18	d	331	8	c	346	7	bc	341	7	bc	370	4	ab	383	7	a	386	7	a
Neck Girth	405	44	c	544	22	b	589	17	b	577	14	b	696	28	a	731	23	a	765	14	a
Chest Girth	626	58	e	821	31	d	900	28	cd	865	19	d	1,021	45	bc	1,074	29	ab	1,157	23	a
Wrist Girth	206	15	c	250	6	bc	276	17	ab	259	6	abc	286	7	ab	286	7	ab	295	6	a
Elbow Girth	290	26	d	363	11	c	369	11	c	389	11	bc	430	14	ab	450	12	ab	469	15	a
Zygomatic Circ.	446	32	d	567	18	c	599	15	c	593	11	c	671	19	b	713	15	ab	750	17	a
Forepaw Width	88	5	e	101	3	d	106	2	bcd	104	2	cd	112	2	abc	119	2	a	116	3	ab
Forepaw Length	86	3	d	96	2	cd	98	2	bc	95	2	cd	106	2	ab	107	3	ab	107	2	a
Hindpaw Width	79	6	d	92	2	c	96	2	bc	97	2	bc	104	2	ab	108	2	a	108	3	a
Hindpaw Length	155	12	c	174	3	b	178	3	ab	179	2	ab	187	3	ab	190	3	a	191	3	a
Canine Length (Upper)	22.9	2.7	d	27.5	0.6	c	29.1	0.4	c	29.5	0.4	abc	30.8	0.8	ab	31.4	0.7	abc	32.4	0.7	a
Canine Length (Lower)	22.5	2.6	b	26.6	0.5	a	27.4	0.3	a	27.8	0.2	a	28.4	0.6	a	29.5	0.5	a	27.3	0.7	a
Canine Width (Upper)	8.9	0.6	c	9.8	0.2	c	10.4	0.1	bc	10.4	0.2	bc	11.2	0.5	ab	11.9	0.5	ab	12.4	0.4	a
Canine Width (Lower)	8.8	0.6	c	10.0	0.2	bc	9.9	0.3	bc	10.5	0.2	abc	11.2	0.3	ab	11.8	0.6	a	11.2	0.3	ab
Canine Breadth (Upper)	49.0	1.6	c	52.3	1.0	c	53.9	0.9	bc	52.9	0.7	c	57.7	1.0	ab	60.0	2.4	a	60.5	1.0	a
Canine Breadth (Lower)	42.0	2.5	d	46.4	0.9	cd	48.5	0.8	bc	48.5	0.5	bc	51.2	0.8	ab	54.4	1.2	a	52.9	0.9	a

¹ Within rows, means followed by the same letter are not different (Tukey's studentized range test, $P > 0.05$).

Table 2. Morphometric characteristics (mm unless otherwise noted) of female black bears significantly affected ($P < 0.005$) by age in Great Dismal Swamp.

Characteristics	Age (years)											
	1 (n=4-7)		2 (n=3)		3 (n=4-6)		4 (n=4)		5 (n=1)		6 (n=3-5)	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Mass (kg)	36.0	4.3	c ²	35.7	4.4	c	51.8	1.2	abc	57.5	3.5 ³	abc
Total Length	1,248	27	c	1,297	87	bc	1,433	29	ab	1,500	20	a
Head Length	271	4	d	285	9	cd	303	3	bc	309	3	ab
Neck Girth	381	15	c	413	22	c	451	16	bc	450	7	ab
Chest Girth	614	34	c	640	44	bc	705	15	bc	740	3	abc
Wrist Girth ⁴	193	8	b	198	11	ab	209	3	ab	219	6	ab
Elbow Girth ⁵	271	9	b	280	10	ab	318	17	a	310	5	ab
Zygomatic Circ.	435	11	d	425	15	bcd	497	11	bc	499	8	ab
Canine Length	21.0	0.8	b	23.9	1.6	ab	25.4	0.7	a	26.0	0.9	a
(Upper)												
Canine Length	21.3	0.9	b	22.8	0.8	a	23.5	0.4	a	23.6	0.4	a
(Lower)												
Canine Width ⁶	7.4	0.1	b	8.2	1.0	ab	8.7	0.3	ab	9.4	0.2	ab
(Upper)												
Canine Width ⁵	7.5	0.3	b	8.8	0.6	ab	8.8	0.3	ab	8.7	0.1	a
(Lower)												
Canine Breadth	43.7	0.9	b	47.1	2.4	ab	47.5	0.5	ab	48.8	0.4	a
(Upper)												
Canine Breadth ⁵	40.3	0.8	b	41.5	1.1	ab	42.6	0.7	ab	43.9	0.2	a
(Lower)												

¹ $P < 0.001$ for all variables unless otherwise noted. ² Within rows, means followed by the same letter are not different (Tukey's studentized range test, $P > 0.05$). ³ $n=2$. ⁴ $P < 0.002$. ⁵ $P < 0.001$. ⁶ $P < 0.005$.

average of 120 and 88 kg, respectively, in Bladen County, North Carolina, (Hamilton 1978) and 102 and 52 kg, respectively, in a bottomland hardwood swamp in eastern Arkansas (Smith 1985). Harvested, adult females from the periphery of Okefenokee Swamp, Georgia, ranged in mass from 46 to 101 kg (Abler 1985). Smith (1985) reported that males reached peak mass by 5 years of age. Although females reached adult stature by age 2 or 3, they continued gaining mass and girth until age 9 or 10. Bears in Great Dismal Swamp became heavier than bottomland Arkansas bears (Smith 1985) by age 6 in males and age 5 in females. Total length and chest girth measurements were also larger for Dismal Swamp males by age 6.

Table 3. Significant ($P < 0.0001$) bivariate regression models with body mass (kg) as the dependent variable for black bears in Great Dismal Swamp, Virginia and North Carolina, 1984–1986.

Sex	Independent Variable (mm)	Intercept	Slope	r^2	Root Mean Square Error	n
Male	Chest circumference	-103.5	0.21	0.95	8.49	59
	Neck circumference	-89.8	0.30	0.94	9.34	59
	Total length	-170.7	0.16	0.72	19.61	51
	Head length	-225.6	0.91	0.78	17.53	59
	Wrist circumference	-102.7	0.73	0.62	22.66	59
	Elbow circumference	-92.5	0.47	0.66	21.59	59
	Zygomatic circumference	-136.4	0.37	0.92	10.57	59
	Forepaw width	-222.9	2.95	0.70	20.31	59
	Forepaw length (no claws)	-201.8	2.95	0.52	25.18	58
	Hindpaw width	-204.7	3.04	0.68	20.80	59
	Hindpaw length (no claws)	-230.2	1.80	0.47	26.89	59
	Canine length (upper)	-153.3	8.40	0.52	25.98	57
	Canine length (lower)	-123.6	7.93	0.25	32.40	58
	Canine breadth (upper)	-293.5	7.03	0.71	20.69	55
	Canine breadth (lower)	-273.4	7.47	0.66	22.12	56
Female	Chest circumference	-57.1	0.15	0.92	3.75	29
	Neck circumference	-55.4	0.23	0.89	4.46	31
	Total length	-68.8	0.08	0.53	9.32	28
	Head length	-119.3	0.56	0.72	7.16	31
	Wrist circumference	-69.5	0.56	0.58	8.76	31
	Elbow circumference	-61.6	0.36	0.70	7.46	31
	Zygomatic circumference	-91.4	0.28	0.86	4.97	31
	Canine length (upper)	-34.1	3.42	0.45	9.84	33
	Canine breadth (upper)	-101.0	3.16	0.52	9.27	31
	Canine breadth (lower)	-144.4	4.56	0.46	9.71	32

Regression analyses indicated that chest girth, neck girth, and zygomatic circumference were the best predictors of body mass for both sexes (Table 3). Chest girth has been used commonly to estimate body mass in bears (Cherry and Pelton 1976, Glenn 1980, Nagy et al. 1984), although Swenson et al. (1987) cautioned that interpopulation variation in measurement-mass relationships makes it impossible to produce a single, species-specific equation. These authors also concluded that gender variation warranted development of sex-specific prediction equations.

Morphometric data can be used to predict nutritional condition (Cattet 1990) and make intraspecific comparisons of body size. Differences in body size and growth rates of black bears of different populations resulting from variability in ecosystem productivity may lead to differences in skull morphometry, a key tool in taxonomic analysis. If morphometric variation between populations is best explained by phenotypic responses to the environment, can morphometrics be used to classify animals into subspecies (Pelton 1990)? Such a question is germane to taxonomy of black bears and other species.

Our paper reports on a single, southeastern Coastal Plain population of black bears. We encourage other black bear researchers to standardize the collection and reporting of data on external morphometrics to maximize their utility.

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Nutrient Content of Squawroot, *Conopholis americana*, and Its Importance to Southern Appalachian Black Bears, *Ursus americanus* (Carnivora: Ursidae)

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ABSTRACT—Squawroot (*Conopholis americana*), a preferred late spring and early summer food of black bears (*Ursus americanus*), was collected from Pisgah National Forest, North Carolina, on a weekly basis from 25 April to 4 July 1987. Proximate analysis procedures were used to determine the nutrient content of the plant. Samples were examined for nutrient differences between the capsule and stems. Peak percentages were 13% crude protein (capsule), 31% crude fiber (capsule), 3% fat [either extract] (capsule), and 77% nitrogen-free extract [NFE] (whole plant). Gross energy averaged 4.84 kcal/dry g. Levels of crude protein, crude fiber, and either extract were similar to values reported for soft mast species eaten by bears, and NFE was greater than herbaceous material consumed in spring. Trends in protein and fat content were higher in the capsules; protein decreased as crude fiber increased. Nitrogen-free extract levels were relatively high throughout the study and likely represent an important energy source for bears feeding on squawroot.

Squawroot (*Conopholis americana*) is a perennial, parasitic plant (Musselman 1982) common to the Piedmont and southern Appalachian (Harvill et al. 1981). Little is known about the plant, but it appears to grow only from the roots of oak trees (Musselman and Mann 1978), probably by infecting young root tips (Musselman 1982).

Squawroot also is a common food eaten by black bears in spring and early summer in the southern Appalachians (Beeman and Pelton 1980, Eagle and Pelton 1983, Garner 1986); the species is locally abundant and may be nutritionally important to bears. Because of its local abundance and time of maturity (often the first productive food available), squawroot patches may influence movements of female bears in the southern Appalachians. By locating readily-available, high-energy foods, females may improve their energy benefit/cost ratio, thereby increasing cub survival. The purpose of this study was to determine the nutritional content of squawroot.

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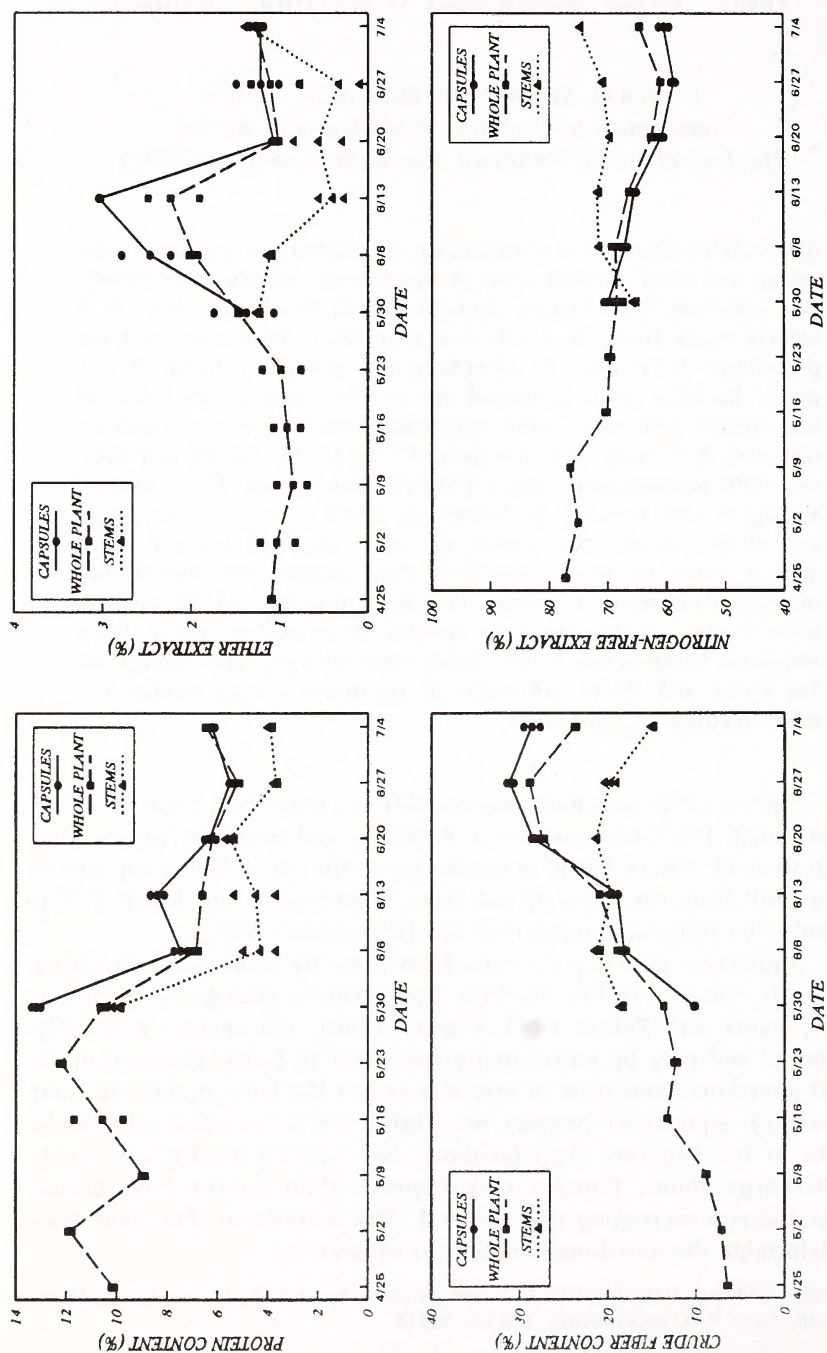


Fig. 1. Nutrient content of squawroot collected weekly on Pisgah National Forest, North Carolina, 1987.

STUDY AREA

The study was conducted on the Harmon Den Bear Sanctuary, Pisgah National Forest, North Carolina. The area is part of the Blue Ridge Physiographic Province (Fenneman 1938). The mountains are sharply dissected and the terrain is steep. Elevations range from 439 to 1,411 m; slopes average over 30% (Finlayson 1957). The area is described as a warm-temperate rain forest (Thornwaite 1948). Vegetation is diverse and changes dramatically with aspect, elevation, soil, and drainage. The general area is among the most botanically diverse temperate areas in the world (Whittaker 1956).

The majority (89%) of Harmon Den is in hardwood cover types, consisting of white oak (*Quercus alba*)-northern red oak (*Q. rubra*)-hickory (*Carya* sp.) (45%), yellow poplar (*Liriodendron tulipifera*)-white oak-northern red oak (26%), yellow poplar (10%), scarlet oak (*Q. coccinea*) (5%), and chestnut oak (*Q. prinus*) (3%) (U.S. Forest Service 1988).

METHODS

Whole plants of squawroot (20–30 plants) were collected weekly from 25 April to 4 July 1987 at elevations ranging from 946 to 1,068 m. Quantities of 639 to 1,123 g were obtained each week; samples were composited, therefore no statistical analysis could be performed. Thus, the trends or differences noted in this paper may not be statistically significant. Oven-dried samples were analyzed for crude protein, crude fiber, nitrogen-free extract, fat (ether extract), and gross energy (Maynard et al. 1979).

Capsules and stems were analyzed separately to detect nutritional differences between them because, as squawroot matured, bears were observed to selectively feed on the capsule portion of the plant. Capsules were difficult to separate from the stem before 30 May.

RESULTS

CRUDE PROTEIN

The trend for crude protein (\bar{x} = 8.8%, SE = 0.51, range = 5.1–12.3%) of the entire plant peaked during late May (Fig. 1). Capsules (\bar{x} = 7.8%, SE = 0.78, range = 5.5–13.4% contained more protein than stems (\bar{x} = 5.5%, SE = 0.58, range = 3.6–10.2) throughout the study. The highest percentage of protein occurred in the capsules collected 30 May. However, much of this protein may have been in the seeds (Wainio and Forbes 1941) and unavailable because bears do not crack or digest the seed coat (Eagle and Pelton 1983).

FAT (Ether Extract)

Fat content in squawroot was low (Fig. 1) and similar to soft mast species such as huckleberry (*Gaylussacia* sp.) and black gum (*Nyssa sylvatica*) (Landers et al. 1979), which also are important to bears. The greatest trend in percentage of fat occurred in the capsules collected on 13 June. Fat trends were higher in capsules ($\bar{x} = 1.53\%$, $SE = 0.14$, range = 1.0–3.0%) than stems ($\bar{x} = 0.75\%$, $SE = 0.12$, range = 0.1–1.4%) for all except the final collection. Mean fat content for the whole plant was 1.34% ($SE = 0.69$, range = 0.7–2.5%).

CRUDE FIBER

The trend in crude fiber for the stem ($\bar{x} = 19.23\%$, $SE = 0.65$, range = 14.8–21.5%) was similar throughout the study (Fig. 1); this might be expected because the stem is the only structural component of the plant. Crude fiber increased in the capsules ($\bar{x} = 22.62\%$, $SE = 2.24$, range = 10.2–31.5%) throughout the study period and appeared negatively correlated with protein. Crude fiber averaged 16.53% ($SE = 1.65$, range = 6.4–29.0%) for the whole plant.

NITROGEN-FREE EXTRACT (NFE)

Nitrogen-free extract was highest in early spring and lowest in late June in the whole plant ($\bar{x} = 69.1\%$, $SE = 1.14$, range = 61.1–77.4%) and capsules ($\bar{x} = 63.7\%$, $SE = 1.23$, range = 58.4–70.7%) (Fig. 1). NFE increased from late May to July in the stems ($\bar{x} = 70.7\%$, $SE = 2.88$, range = 65.1–74.9%).

GROSS ENERGY

There was little variation in gross energy among weeks, or between the different plant parts; this agrees with Robbins (1983) and Powell and Seaman (1990). Gross energy averaged 4.8 kcal/dry g ($SE = 0.03$, range = 4.7–5.1) (whole plant); 5.0 kcal/dry g ($SE = 0.05$, range = 4.9–5.2) (capsules); and 4.7 kcal/dry g ($SE = 0.06$, range = 4.3–5.0) (stems).

The nutritional content of squawroot appeared to change over time. Protein and nitrogen-free extract (NFE) concentrations were greatest during the early weeks. Fat was greatest during middle of the study, and crude fiber was lowest early and increased with time.

DISCUSSION

Spring diets of bears in the southern Appalachians contain large amounts of herbaceous material (Beeman and Pelton 1980, Eagle and Pelton 1983, Garner 1986). Herbaceous material is relatively high in protein (Landers et al. 1979, Eagle and Pelton 1983). Nitrogen-free

extract, however, is lowest in spring foods (Landers et al. 1979). Eagle and Pelton (1983) suggested that squawroot was probably an important energy source for bears because the carbohydrates in squawroot are readily absorbed.

Squawroot is likely a major source of carbohydrates (represented by relatively high NFE concentrations) in the spring diet of bears in the Harmon Den area. Nitrogen-free extract concentrations in squawroot tended to remain relatively high throughout the study, and carbohydrates available in squawroot appear to be easily absorbed (Eagle and Pelton 1983); this may be important to a bear's overall spring and early summer condition. The combination of high protein herbaceous material and relatively rich carbohydrate squawroot may be important for bears recovering from the denning period; particularly for lactating females with cubs, because of their increased nutritional requirements (Eagle and Pelton 1983, Rogers 1987).

The habitat types where squawroot occurs (i.e., mature oak stands) should receive special concerns, as management of these stands for peak acorn production also would maintain ample sources of squawroot for bears throughout their range in the southern Appalachians.

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NEW PUBLICATION

Bird Life of North Carolina's Shining Rock Wilderness is the most recent release in the Occasional Papers of the North Carolina Biological Survey series published by the North Carolina State Museum of Natural Sciences. Written by Marcus B. Simpson, Jr., M.D., of the George Washington University Medical Center, Washington, D.C., the work summarizes the geomorphology, climate, vegetation, and ornithological exploration of the wilderness area and presents an annotated list of 130 species known to occur within its boundaries. Illustrations include a map of Shining Rock Wilderness and adjacent Middle Prong Wilderness, both managed by the United States Forest Service, an agency of the U.S. Department of Agriculture. The 32-page soft-cover book sells for \$5 postpaid. Send orders to: Publications Secretary, N.C. State Museum of Natural Sciences, P.O. Box 29555, Raleigh, NC 27626-0555. Make checks payable (in U.S. dollars only) to Museum Extension Fund.

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